BINARY VARIATION IN TRADESCANTIA BRACTEATA

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Although it is peculiarly variable, *Tradescantia bracteata* is ordinarily one of the most distinctive and easily recognized of the dozen or so species which are closely related to *T. virginiana*. In addition to various minor characters, it differs from all these species by its long rhizomes which permit it to grow into large mat-like clones, even in prairie sod. Plants of this species in an experimental garden may spread to a diameter of two or three feet, while in the same period the growth of other species is to be measured by inches, if at all.

In spite of its several distinctive features, *Tradescantia bracteata* is somewhat variable in a peculiar sort of way. If one confines his study to the selections from populations which find their way into herbaria, the variation seems no more extreme or extensive than in the other widespread species of *Tradescantia*. If living populations (or mass collections) are examined, however, it will be found that they vary around two quite different centers which are illustrated in figs. 1 and 2. In the prairie populations which we have studied the bulk of the individuals are more or less similar to Type 'A'. They have unusually vigorous rhizomes and form large clones. The flowering stems are unbranched, and there are usually four

long internodes above the ground level. The leaves are narrow with a peculiar yellowish cast, and the pubescence tends to be very short and scattered. The other center (Type 'B') is made

Fig. 1.   Habit sketch of *Tradescantia bracteata*, type 'A.'

up of plants which tend to be characterized by broad leaves, fewer nodes to the stem, vigorous secondary branches, and a lesser capacity to spread into large clones. If collections are made only by the tens and twenties these two centers are apt

Fig. 2.   Habit sketch of *Tradescantia bracteata*, type 'B.' Figs. 1 and 2 drawn to the same scale by Ruth P. Ownbey, from plants collected at Portage des Sioux, Mo.

to appear, but in every collection of 100 or more plants from the same colony they are certain to be evident.

Tradescantia bracteata is therefore unique among the American Tradescantias because it exhibits extreme *intra-regional* variation. There are other species of *Tradescantia* which show as much variation when collections are made from widely different regions within their ranges, but we have found no other species which varies in this way within single populations.

To analyze this variation, mass collections of *T. bracteata* were made at a number of points. The collection at Portage des Sioux was studied the most intensively since it was nearest the laboratory, but the general features discovered there are similar at the other points where a large population was analyzed. Extremes of the two types illustrated in figs. 1 and 2 were studied carefully, and from them an index was constructed for classifying the entire population with reference to the approach of each individual to these two types. The method was originally worked out for studying hybrid populations of *Tradescantia* (Anderson, '36) and has been found to be generally applicable to such cases. The particular characters used in this index and the values assigned to each are as follows:

Maximum width of floral leaves:
  Over 19 mm. 0
  Under 19 mm. 4

Sepal color:
  Florid 0
  Intermediate 1
  Not florid 2

Stomata (under a hand lens) :
  More conspicuous than surrounding cells 0
  Scarcely as conspicuous as surrounding cells 1
  No more conspicuous than surrounding cells 2

Number of elongated internodes on the flowering stems:
  2.. 0
  3.. 1
  4 or more 2

Branching of the flowering stem:
    Unbranched................................... 2
    With sterile branches 1
    Branches bearing flowers 0

This index was used in classifying four populations of *T. bracteata*, with broadly similar results in each case (fig. 3), but with significant special features. At each of these localities the species was found to be morphologically duplex. That is to say, that it fluctuated around two different centers, Type 'A' and Type 'B'. That these two types are due to inherent differences in the germplasm and not to environmental or age differences is shown by the fact that transplants have consistently maintained their original type in the experimental garden. Plants moved from various midwestern points to Boston and from the Dakotas to St. Louis have held to their original type over a period of years.

Although connected in each population by a manifold series of intermediates, the extremes when sorted out by means of the index were most surprising. Individually or as a group, the extreme plants of Type 'B' are morphologically very similar to *Tradescantia hirsutiflora* of the Gulf Coast, a species which is today completely unknown within the range of *T. bracteata*.

Tradescantia hirsutiflora (or at least one element in it) is itself so similar to *T. virginiana* that it might almost be considered a geographically localized variety of that species. While the ranges of *T. virginiana* and *T. bracteata* overlap slightly, extreme plants of Type 'B' resemble *T. hirsutiflora* more closely than they do *T. virginiana*.

In any explanation of the binary variation of *T. bracteata*, there are several critical pieces of evidence.

1. While the differences between the two types are manifold, there is enough relationship physiologically between them to suggest that there might be basically a single difference in rhizome vigor, to which all the other differences are secondary. Active rhizomes would produce large clones with many shoots, among which there would be more root competition beneath
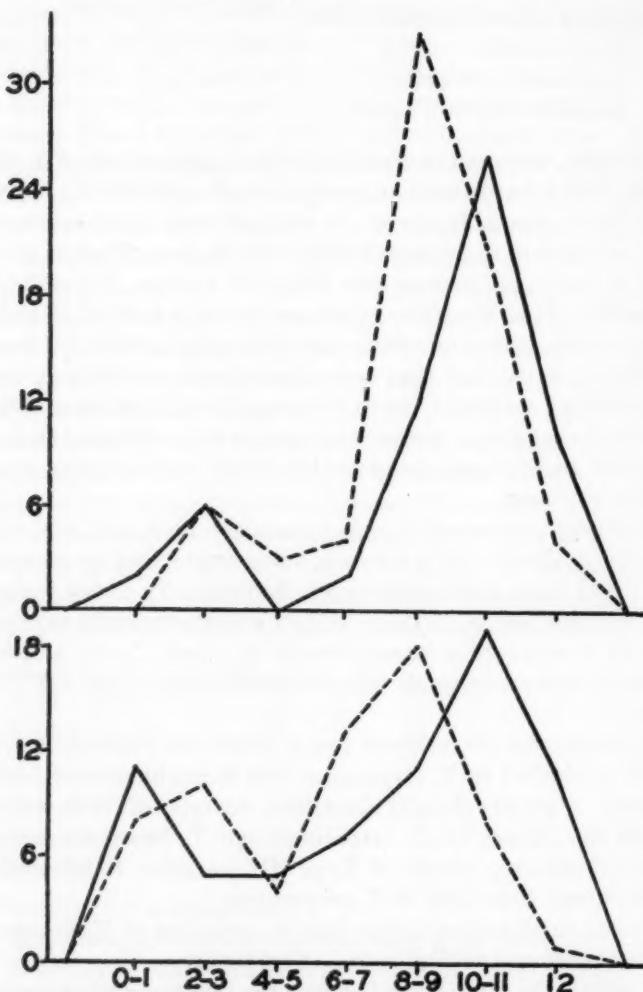
Fig. 3.   Frequency diagrams for Index No. 1 of four populations of
T. bracteata. Upper figure, from plants growing in sod: dotted line, 60
plants from unplowed swamp pastures at Portage des Sioux, Mo.; solid
line, 30 plants from prairie swale at Harris's Grove, north of Grinnell,
Iowa. Frequencies crudely adjusted by multiplying by 2. Lower figure,
two populations from roadways: dotted line, 60 plants along roadway at
edge of field, Portage des Sioux, Mo.; solid line, 60 plants from railroad
right-of-way and roadway, Victor, Iowa.

the soil and more shading above the soil. It is therefore conceivable that the narrower, less-branched shoots and the narrow leaves and smaller flowers might be merely a secondary consequence of more active rhizomes.

2. Though the differences between the two types might result from a single physiological difference, there is little in the variation to suggest that it is the work of a few genes. The differences are too manifold and the variation of the intermediates resembles the varied recombinations of second-generation species crosses rather than simple Mendelian segregation.

3. The differences are apparently not due to age, since transplants of both types have maintained their original character when brought into experimental gardens. One of the clones which was originally selected because of its remarkable capacity to spread repeated this behavior when transplanted from Iowa to Massachusetts.

4. The peculiar characteristics of Type 'A' are unique in this group of species.

From this evidence we conclude that Type 'A' and Type 'B' owe their differences to segregating elements within the germplasm, to differences of the order of whole chromosomes or of chromosome arms. As to how this variation was introduced into the species we have no evidence. There are at least two very different ways in which it might have occurred. On one view, *Tradescantia bracteata* would originally have been only of Type 'B'; on the other hypothesis, the original element in the species would have been Type 'A'. It may be that the binary condition is as old as the species. On that view, the peculiarities of Type 'A' appeared within the original primitive stock of Type 'B' (by whatever process or group of processes specific differences are achieved in this genus) with the added peculiarity that the original stock tended to be carried along in the population. Quite another hypothesis is suggested by the resemblance of the variation of *T. bracteata* to that which we have studied in species hybrids of *Tradescantia*. On this view, Type 'A' was originally differentiated as a unique species and Type 'B' then originated by hybridization between Type 'A' and *T. hirsutiflora* at a time when the ranges of one

or both of these species were different enough from their present distributions to bring them into contact. If this happened comparatively recently we might expect to find Type 'B' limited to the southern or southeastern extremity of the range of
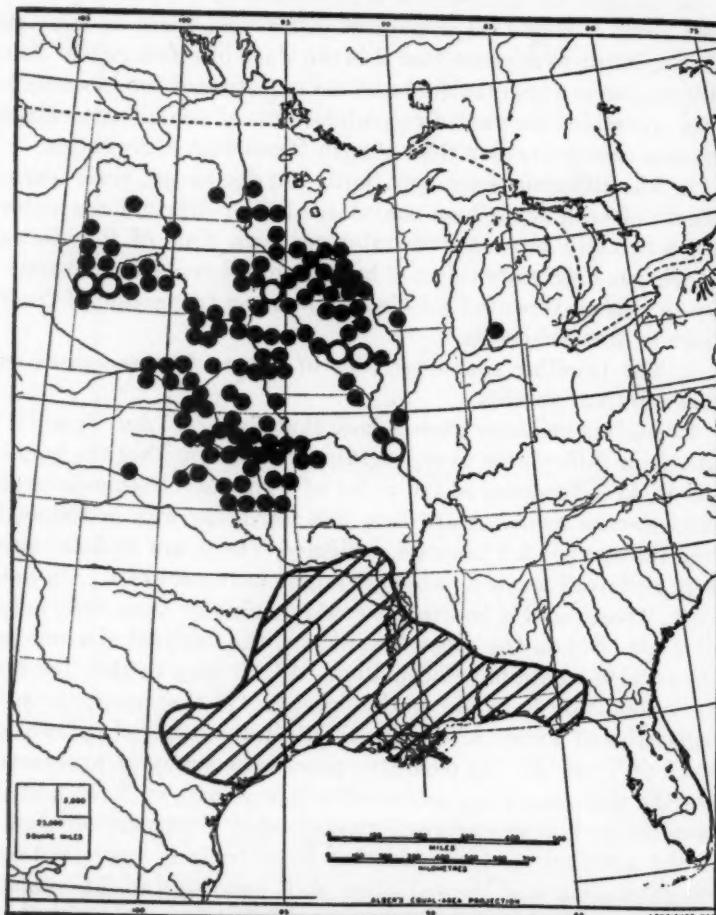

Fig. 4.   Map of middle-western United States showing the known distribution of *T. bracteata* (black dots) in relation to that of *T. hirsutiflora* (diagonal lines). Each dot represents an herbarium specimen; open circles, points at which mass collections were made.
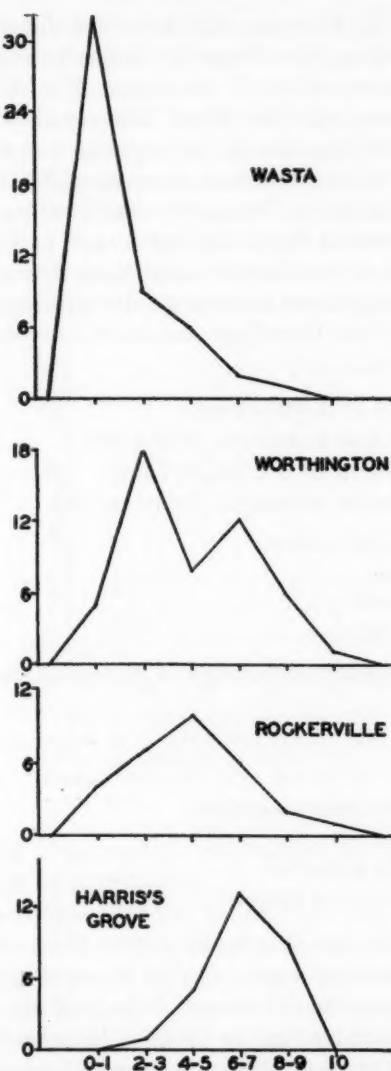
Fig. 5. Frequency diagrams for Index No. 2 of four populations of *T. bracteata*. Populations arranged according to the percentage of open soil in the habitat.

T. bracteata. If, however, the hybridization is a matter of
very long standing, then Type 'B' might be expected to occur
throughout the range of *T. bracteata.* For determining this
point collections from the Black Hills would be particularly
significant since they are at the opposite end of the range of
T. bracteata. Mass collections were accordingly made at the
points shown in fig. 4. Frequency distributions for these col-
lections are shown in fig. 5. The index used in deriving the fre-
quencies for fig. 3 could not be used since it was based in part
on characters which can be scored only in living material. The
following index was therefore constructed for dealing with the
pressed material:

Maximum width of floral leaves:
    From mid-vein to margin, over 8 mm. 0
    From mid-vein to margin, 6–7 mm. 1
    From mid-vein to margin, 5 mm. or less 2

Length of hairs on pedicel:
    Over 0.8 mm. 0
    0.5 to 0.7 mm. 1
    Less than 0.5 mm. 2

Number of elongated internodes on flowering stems:
    2. 0
    3. 1
    4 or more 2

Branching of the flowering stem:
    Unbranched. 2
    With sterile branches 1
    Branches bearing flowers 0

It will be seen that this index differs from that previously
used in the following ways: (1) In measuring the maximum
width of the floral leaves (bracts) one-half the width rather
than the whole width had to be used because the specimens
were pressed. This, as well as the changes in drying, increases
the percentage of error. (2) The color of the sepals and the
character of the stomata could not be ascertained in pressed
material. In their place the length of the pubescence of the

pedicel was substituted, since it is prevailingly thick and long in Type 'B' and short and scattered in Type 'A.' It was measured to a tenth of a millimeter, using a camera lucida. The measurement was accurate, but a study of plants in the experimental garden has shown that this character is affected by temperature and humidity. Index No. 2 therefore, while it is more or less similar to Index No. 1, is not as accurate, and since it is based on fewer characters does not separate the two centers as well in the frequency distributions. However, it gives a roughly similar result as will be seen from fig. 6, which shows
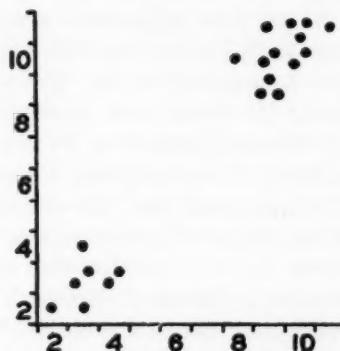

Fig. 6. Correlation between index values of 20 plants from Portage des Sioux as measured by Index No. 1, vertical scale, and Index No. 2, horizontal scale.

the correlation between the two indices for 20 plants which were measured by each index.

Population frequencies for Index No. 2 are graphed in fig. 5. It will be seen that Type 'B' not only occurs in the opposite corner of the range of *T. bracteata* from that which comes closest to the territory of *T. hirsutiflora* but that it even makes up a higher percentage of the population than it does in the south. This is perhaps correlated with open-soil habitats and is discussed below on page 159. The curves are also less bimodal than in the Missouri and Iowa populations. This is in part due to the inferiority of the index but probably also re-

flects a real difference in the northwestern populations. How-
ever, although plants of Type 'A' were not present in large
enough numbers to produce a bimodal curve, at least a few
were encountered at every locality as well as various inter-
mediates. Type 'B' therefore most probably originated be-
fore *T. bracteata* moved into the territory it now occupies.
The entire group of species to which it belongs is centered
upon the Edwards Plateau in east-central Texas. It is quite
possible that at one time *Tradescantia bracteata* grew within
this same general area and could then have differentiated from,
or hybridized with, *T. hirsutiflora*. This latter species still
occurs there and is the most aggressive species in that area
and the one most apt to hybridize with other species.

To summarize: Associated with typical *Tradescantia
bracteata* throughout its range and connected with it by a
manifold series of intermediates is a *Tradescantia* morpho-
logically very similar to *T. hirsutiflora,* a species of the Gulf
Coastal Plain. It is suggested that this variant originated by
partial differentiation from, or hybridization with, *T. hirsuti-
flora* at a time when the two species were in closer contact
than now, and presumably before *T. bracteata* moved into the
territory it now occupies. Since the chief effect of the phe-
nomenon is to produce a species which fluctuates around two
centers, instead of one, we are calling it *binary variation.*

There now remains to discuss:

(1) Its selective advantages.

(2) The cytology of *T. bracteata*.

(3) Its probable occurrence in other groups of organisms.

(1) *The selective advantages of binary variation.*—As will be
seen from the map in fig. 4, *Tradescantia bracteata* is a spe-
cies of the prairies and northern great plains. This region is
notorious for a climate which fluctuates widely from decade
to decade as well as from year to year, and within that area
Tradescantia bracteata is most commonly found in marginal
habitats which are peculiarly susceptible to climatic fluctua-
tions. In the prairie states it grows at the edges of swales or
in slight depressions which are just damp enough to discourage

some of the prairie grasses. A single dry year has a marked effect upon the vegetation. In a fluctuating climate, in such a habitat, a species which varies around two centers would be at a great selective advantage, particularly if the permanence of the two-centered condition was assured by some cytogenetic mechanism. In this connection the frequency curves of fig. 3 are rather suggestive since they demonstrate that with a slight change in habitat there are changes in the proportions of Type 'B'. Two populations were studied in Missouri and two in Iowa. In each case one of the populations was from a more or less natural prairie and the other was from a man-made habitat. At Portage des Sioux, Missouri, in rich bottomland near the junction of the Mississippi and Missouri rivers, is a low grassy pasture which is apparently a remnant of one of the river-bottom savannahs once common to the region. One collection was made in the pasture and another along a cart track which ran beside it. Of the Iowa collections, one was from the edges of a grassy swale in an unplowed pasture and the other from along a railroad track adjacent to rich bottomland, all of which was under cultivation. It will be seen that the curves of the two prairie habitats are very similar, as are also those of the two trackways, but that the proportion of Type 'B' is much higher in the open-soil habitats, so much so that the make-up of the species differed much more markedly between neighboring habitats than it did between Missouri and Iowa, for the same habitat.

This impression is confirmed by the frequencies for Index No. 2, diagrammed in fig. 5, where they are arranged from above to below according to the prevalence of grass at each locality. At Wasta, North Dakota, there was practically no grass, and many of the plants of *T. bracteata* were growing in soil as open as if they had been cultivated in a garden. At Harris's Grove, the other extreme, the plants were growing in dense prairie sod and were so overtopped by the grass that they were hard to find. The frequency diagrams show that the grassier the habitat, the greater the percentage of Type 'A' and intermediates resembling it. This is not surprising since in at least two ways Type 'A' is evidently better adapted to such an en-

vironment. In the first place, its longer, more numerous inter-
nodes allow it to compete for sunlight with the grasses in situ-
ations where plants of Type 'B' would be completely sub-
merged. In the second place, its extremely active rhizomes
would allow it to compete with the notoriously vigorous rhi-
zomes of the prairie grasses.

(2) *The cytology of T. bracteata.—Tradescantia bracteata* is
prevailingly diploid, with 6 pairs of chromosomes. Table ɪ lists
the chromosome determinations which have been made as well
as those previously listed by Anderson and Sax ('36) and
summarizes the total frequencies. The species is overwhelm-
ingly diploid, although polyploid individuals have been col-
lected in nature at two points. It is therefore unlike all the
other widespread species closely related to *T. virginiana,* since
they are either known only as tetraploids or have diploid races
confined to a relatively small area. There are other diploid
species in this group but, without exception, they are of very
limited distribution and several of them are on the verge of
extinction. In our opinion diploidy has persisted in *T. brac-
teata* because it is actually at a selective advantage in prairie
habitats by reason of its effect upon the flowering season. Like
many other prairie plants, *Tradescantia bracteata* dies down
rapidly after it has flowered and spends the summer in a dor-
mant or semi-dormant condition. In an experimental garden

TABLE I

CHROMOSOME NUMBERS OF PLANTS OF *T. BRACTEATA* COLLECTED
IN THE WILD

Localities	2n	3n	4n	Localities	2n	3n	4n
Houlton, Wisconsin	1			St. Louis, Missouri	1		
Preston, Minnesota	1			Huron, South Dakota	1		
Rock Co., Minnesota	1			Kennebec, S. Dak.	1		
Worthington, Minn.	1			Murdo, S. Dak.	1		
Grinnell, Iowa	3	2		Rockerville, S. Dak.	1		
Kellogg, Iowa	1			Wind Cave, S. Dak.	1		
Kendallville, Iowa	1			Wasta, S. Dak.	2		
Pierson, Iowa	1			Overton, Nebraska	1		
Tama, Iowa	3			Royal, Nebraska	1		
Victor, Iowa	1			Lawrence, Kansas			2
Portage des Sioux, Missouri	8			Manhattan, Kansas	3		

it withers so quickly that one who did not know the species would assume that the plants were badly diseased. Tetraploidy would be disadvantageous to such a species since it favors longer flowering seasons. In nature, in the experimental garden, and in the greenhouse, tetraploid Tradescantias differ from their related diploids, among other things, by the greater length of their blooming periods. Polyploid strains, such as the plants reported in Table I, would be at a selective disadvantage since they would come into flower more slowly and carry their flowering into the unfavorable drought and heat of the summer months. The two tetraploid plants reported above were discovered under precisely those circumstances. When originally collected they were the only plants still in flower at that locality, all the neighboring plants having withered and died down.

Aside from the gross information concerning chromosome number, little is known with regard to the cytology of *T. bracteata*. Sax ('37) and Darlington ('37) have reported inversions in this species, and Swanson ('40), from these facts and his own evidence, has concluded that the occurrence of inversions in *Tradescantia* is very widespread.

The fact that both Type 'A' and Type 'B' have been found in every population which has been examined leads us to suspect that the binary condition is being maintained by some fairly precise cytogenetic mechanism. Otherwise it is difficult to see how both varieties could be present in every population. There must at least be some mechanism by which plants which are phenotypically like one variety can yield offspring resembling the other when they are intercrossed. One would need to postulate no more intricate mechanism than those already demonstrated for cereal rogues or the complexes of *Oenothera*.

Although the morphological differences between the two species seem to be manifold, it is possible, as we have pointed out above, that only a small proportion of the germplasm is responsible for the change. Given the basic difference in rhizome growth, many of the other differences might automatically follow. A large matted clone with many flowering stems might be expected to have narrower leaves and less sec-

ondary branches than an isolated plant such as Type 'B,' with only a few flowering stems. If only one or two chromosome segments are responsible for the bulk of the differences between the two varieties it would be comparatively easy for the binary condition to be maintained.

(3) *Probable occurrence of binary variation in other groups of organisms.*—Binary variation, in our opinion, is probably fairly widespread in both the plant and animal kingdoms. Its frequency can scarcely be discussed until more species have been examined by populations. Up to the present not more than a handful of species has been studied in this way. Certain of the Drosophilae studied by Dobzhansky, Spencer, Patterson, and their students are perhaps to be classified in this category though data with regard to populations are still too meagre to permit a definite opinion. The relationship between the black and white races in the southeastern United States is very similar and differs only in the fact that there are numerous communities which fluctuate around only one center and that the chief isolating factor (social prejudice) has caused nearly all the intermediates to be classified as black instead of being recognized as intermediates.

Among the higher plants binary variation probably occurs fairly frequently within a part of the range of widespread species, but cases such as *T. bracteata* where a species is binary throughout its range are probably rare. In eastern North America many, if not most, of the deciduous trees which are relatively uniform in the North and East include other elements within their populations in the Ozarks and the Southwest. *Acer saccharum,* for instance, forms relatively uniform populations to the northeast, while in the Ozarks usually it includes the variety *Schneckii* and is united with it in that region by a series of intermediates.

SUMMARY

1. Associated with typical *Tradescantia bracteata* throughout its range and connected with it by a manifold series of intermediates is a *Tradescantia* morphologically similar to *T. hirsutiflora.*

2. It is suggested that this variant originated by partial differentiation from, or hybridization with, the *T. hirsutiflora-virginiana* stock at a time when the ranges of these Tradescantias were confluent.

3. The phenomenon is named "binary variation." Its selective advantages and probable occurrence in other species are discussed.

4. The cytology of *Tradescantia bracteata* is discussed. It is suggested that the exceptional maintenance of widespread diploidy in this species is due to the fact that in a prairie and great-plains environment the shorter blooming season of the diploids may be at a selective advantage.

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ON THE FLORA OF THE FRONTIER FORMATION OF SOUTHWESTERN WYOMING[1]

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INTRODUCTION

In 1917 Dr. F. H. Knowlton described a small flora from the Upper Cretaceous Frontier formation of southwestern Wyoming. Attracted by that author's figures of *Microtaenia paucifolia* (Hall) Knowlton, we made a small collection of the fructifications in the summer of 1934. Nothing of exceptional note was obtained at that time and our collections did not receive immediate study. In the summer of 1939, when the senior author revisited the locality, certain undescribed fructifications were discovered, but as time did not permit extensive exploration we returned the following summer and prospected the outcrop carefully for about 4 miles north and 1½ miles south of Little Muddy Creek. We were fortunate in obtaining nearly complete fertile pinnae referable to *Anemia Fremonti* Knowlton and in finding certain other fossil plants or parts thereof not previously described.

The plant-bearing horizon was originally discovered by Capt. John C. Fremont in 1843 while exploring for a better emigrant route to the Northwest. Fremont's collections were turned over to James Hall, New York State Paleontologist, who published descriptions in 1845. Other collections were made at later dates by members of the U. S. Geological Survey and were presented in Knowlton's paper of 1917.

Of the 25 described species composing the flora there are 7 ferns, 1 *Equisetum*, and 17 Angiosperms, the latter including *Quercus*, *Ficus*, *Salix*, *Aralia*, *Dewalquea* and *Cinnamomum*.

Certain of these genera are undoubtedly valid; others are questionable as Knowlton himself admitted. The present paper will not be concerned with the Angiosperm element of the flora.

GEOLOGY

The section of the Frontier formation discussed in this paper is situated in the southwestern corner of Wyoming, about 15 miles south of the town of Kemmerer, in the vicinity of Cumberland Gap. The formation, which consists of a series of light-colored coal-bearing sandstones and shales approximately 2500 feet thick, extends for many miles both north and south of Cumberland Gap and is characterized by a series of prominent hogbacks. It is underlain by the dark-colored oil-bearing Aspen shales, and overlain by the dark-colored Hilliard shales. The most prominent hogback is formed by the Oyster Ridge member, which is an oyster *(Ostrea soleniscus)*-bearing sandstone about 200 feet thick near the top of the formation. Numerous coal seams are contained in the lower half of the formation.

The plant material was collected from a series of white to light blue-gray shales about 50 feet thick. These are located stratigraphically about 75 feet above the generally accepted base of the formation. Small sandstone beds directly above the plant-bearing shales contain a great deal of silicified wood. The plant shales break poorly along the bedding plane and are in the nature of argillite which in thin section is a typical clastic, fine-grained sediment consisting of approximately 70 per cent clay minerals, 28 per cent angular quartz, 1 per cent feldspar, 1 per cent zircon, hornblende, biotite and carbonate (Veatch, '07).

METHODS

The cellulose transfer technique proved very satisfactory with the compressions of the fertile pinnae of *Anemia Fremonti* (see p. 168). Fragmentary specimens were selected in which the fructifications appeared to be well preserved. A

rather heavy coat of nitrocellulose solution (Darrah's formula) was then applied to the surface of the matrix and exposed plant material. The entire specimen was then placed in hydrofluoric acid. It was found advisable not to cut away the apparently excess rock in back of the compression because in some cases this contained additional fragments of the fructifications which dissolve away from the rock and serve as excellent material for maceration.

The disintegration of the rock can be accelerated by removing the block from the acid each day and scraping away the partially dissolved matrix. Specimens as thick as 1½ inches were treated in this way, and the time for complete dissolution

TABLE I

GEOLOGIC COLUMN SHOWING THE RELATION OF THE FRONTIER FORMATION TO OTHER CRETACEOUS FORMATIONS (FROM VEATCH, '07, TABLE FACING p. 501)

System and Group			Formation
Eocene			Unconformity
Cretaceous	Colorado	Lower Laramie	Adaville formation, with basal Lazeart sandstone
		Montana	Hilliard formation
		Niobrara	
		Benton	Frontier formation with the Oyster Ridge sandstone member
			Aspen formation
		Bear River, Dakota?, and Lower Cretaceous?	Bear River formation
			Beckwith formation
	Jurassic		Twin Creek formation

of the rock was in no case longer than 10 days. The last fragments of matrix may be removed with a camel's-hair brush under water. This transparent celloidin technique had, with our material, two very important advantages: first, the back side of the fossil may be studied as well as the front when it is mounted; and second, much better photographs could be obtained than when the rather grayish rock matrix constituted the background. If figs. 2 or 3 (photographs of specimens in the matrix) be compared with figs. 1 and 5 (photographs of specimens transferred to celloidin) the difference is quite apparent.

Maceration of the isolated fragments of the fructifications was done in the usual way with strong nitric acid and potassium chlorate.

SCHIZAEACEAE

Anemia Fremonti Knowlton forma **fertilis** Andrews, forma nov.

It is not often that well-preserved spore-bearing parts can be referred with certainty to any of the numerous sterile fern species that go to compose the fossil record. Associated with foliage which Knowlton ('17) described as *A. Fremonti* were found fructifications of an undoubted schizaeaceous nature and, as will be made clear, in all probability referable to the genus *Anemia*. The significance of the association of fertile and sterile parts will be considered after the former have been described.

The most complete specimen that we have found is shown in fig. 3. It is pinnately compound, the branching taking place in one plane. Figures 1, 2, 4, 5 are isolated primary branches (as will be shown below, these are secondary pinnae, according to usual fern terminology) photographed at a higher magnification. The secondary branches, which are quite short, bear two or three flattened globose bodies, two being borne laterally and a third terminating the branch. In figs. 2 and 5 only one of these bodies may be seen attached to each secondary branch; in fig. 4 two may be seen on some branches while others have only one, both the terminal and a lateral having been lost.

Well-preserved fragments of the primary branches isolated from the matrix show three in all cases.

Within one minute after such fragments had been treated with strong nitric acid and potassium chlorate each of the small black bodies opened up into about seven "valves." If maceration was not then stopped by diluting the acid with water, the fragments very soon almost completely disintegrated. Due to the extreme fragility of the material at this point it has not been possible to prepare permanent preparations nor to obtain satisfactory photographs. Figure 36 shows a secondary branch with its three "bodies" opened out. The segments referred to as valves are in fact pinnules and bear sporangia on their inner surface.

In only one or two cases has it been possible to detect the segmented (pinnular) nature of the globose bodies prior to maceration. The separation of the individual pinnules upon maceration is, however, always uniform and can in no wise be attributed to a maceration artifact. In only two instances have all of the sporangia been observed in place on a pinnule, one of which is shown in fig. 38. The sporangia are arranged in two rows, forming the typical monangial sori of the Schizaeaceae. No evidence of an indusium has been observed. Upon further maceration the sporangia go almost completely to pieces. The maceration residue, however, reveals two structures of considerable interest, spores and more or less complete annuli.

The spores (figs. 6–12) are beautifully preserved, the entire exine being sculptured with characteristic ridges. These are well brought out in the photographs of opposite sides of the same spore (figs. 7 and 8). The triradiate commissure is well defined. Of 50 particularly well-preserved spores that were measured, the average diameter was found to be 40 μ. There is, however, considerable range in size of the spores (from 25 to 47 μ in diameter), as may be noted from the figures where all are shown at the same magnification.

The annuli are also abundant in the residue, the rest of the sporangia disintegrating almost completely. Due to their opaque nature the annuli (fig. 33) are not the best of photo-

graphic subjects and are always split open, apparently along the stomium.

It may be seen then that the structures referred to above as primary and secondary branches are, according to usual fern terminology, secondary and tertiary pinnae, and the sporangia are borne on the under-surface of the ultimate divisions or pinnules. The structure of the pinnules, arrangement of the sporangia, nature of the annulus, and characteristic sculpturing of the spores leave no doubt as to the schizaeaceous affinities of the fossil, and of the four living genera of the family, it is clearly more closely related to *Anemia* than any of the other three. The specimen shown in fig. 3 is comparable in every respect with one of the two basal fertile pinnae characteristic of the species of that genus.

The authors are well aware of the inadvisability in general of placing great weight on the association of isolated parts of fossil plants. In this case, however, the above-described fructifications were found associated with, and only with, the foliage described by Knowlton as *Anemia Fremonti* (figs. 35, 39). The two were found together at three different points between ¼ and ½ mile south of Little Muddy Creek. A comparison of the sterile frond (fig. 39) with certain living species such as *Anemia adiantifolia* Swartz in itself leaves little doubt as to the validity of Knowlton's generic identification. This similarity, combined with our discovery of fertile pinnae whose characteristics clearly point to the same genus and which are constantly associated with the foliage, stands as a credit to Knowlton's original identification and seems to render superfluous a new specific name for the fertile specimens.

The evidence at hand strongly supports the supposition that these sterile and fertile parts are one and the same species, but in view of the lack of organic connection it is advisable to employ some sort of nomenclatorial segregation. To assign a new specific name to the fertile parts tends to defeat rather than enhance the ideals of such an investigation, and, moreover, implies a distinction that the available evidence does not support. In accordance with the remaining element of doubt we

propose to designate the fertile specimens as a distinct form, namely forma *fertilis*. The problem of interpreting the association of scattered parts of fossil plants is one that the paleobotanist frequently encounters, and it is probably true that most workers are inclined to place too much weight upon such associations. We believe that the procedure employed here does not exaggerate the truth yet does reflect the implications that the evidence affords.

It has been assumed in the restoration (fig. 40) that the specimen shown in fig. 3 is a nearly complete fertile pinna and that the pinnae were borne in pairs as in the modern species. It is quite certain that fig. 3 represents a fairly young pinna since fragments of comparable size when macerated still contained large quantities of spores; furthermore other pinnae have been found, a single secondary one being shown in fig. 4, in which the whole has elongated considerably.

The largest fragment of foliage that we have found is shown in fig. 39. This and numerous other specimens served as the basis of the restoration of the sterile portion of the frond. It may be that the lower sterile pinnae were more deeply dissected than is actually represented.

Fossil history of the Schizaeaceae.—

Our knowledge of the earliest members of the Schizaeaceae has been considerably augmented by the recent researches of Radforth ('38, '39). He has shown that *Dactylotheca Sturi* Sterzel and *D. plumosa* Artis are actually annulate and consequently referable to *Senftenbergia*. There has, in the past, been some doubt as to the affinities of that genus but Radforth's investigations leave no doubt as to its proper inclusion in the Schizaeaceae.

The discovery that *Senftenbergia (Dactylotheca) Sturi* has annulate sporangia extends the history of the family back into Lower Carboniferous (Carboniferous Limestone Series) times. The apical annulus consists of a single row of cells in the modern genera *Anemia, Schizaea* and *Lygonium*. However, Radforth has shown that *Senftenbergia pinnaeformis*, an Upper Carboniferous form, had an annulus of two rows of

cells, while *S. Sturi,* from the Lower Carboniferous, has a less regular annulus 4 to 5 cells deep. Of particular interest to the present discussion is his conclusion "that a close phylogenetic relationship exists between these fossil Schizaeaceae and the living Schizaeaceae, and of the latter, particularly the genus *Aneimia.*"

In Jurassic rocks the genus *Klukia* is an undoubted representative of the family and seems to have been rather widespread, specimens having been reported from Yorkshire, Poland, Caucasia and Korea (?).

From the Lower Cretaceous of Virginia, Berry ('11) has described a fertile frond under the name of *Schizaeopsis expansa* (Font.) Berry. This fossil is rather closely comparable to living species such as *Schizaea elegans,* judging from the general morphology of the frond and the sculpturing of the spores.

Stopes and Fujii ('10) described a schizaeaceous fern, *Schizaeopteris mesozoica,* from the Cretaceous of Japan which seems closest to *Anemia.*

Much just criticism has been aimed at the determination of fossil plants based on sterile material but confirmation of Knowlton's identification of *Anemia Fremonti* indicates that even with sterile foliage all is not guesswork. In view of this confirmation in the case of the Frontier formation species we have checked through Knowlton's ('19) list of supposed species of *Anemia* from America. Judging from the published figures there is a reasonable degree of certainty that the following are correctly referred to that genus:

Anemia elongata (Newberry) Knowlton—
  Laramie formation, uppermost Cretaceous: Erie, Colo. (?), Point of Rocks, Wyo. (?). (Knowlton, F. H., U. S. Geol. Surv. Prof. Paper 130: *pl. 2, fig. 2.* 1922).

Aneimia eocenica Berry—
  Lagrange formation, basal Eocene: Puryear, Tenn. (Berry, E. W., U. S. Geol. Surv. Prof. Paper 91: *pl. 10, fig. 2, pl. 11, figs. 1, 2.* 1916).

Anemia hesperia Knowlton—

Fruitland formation, Upper Cretaceous: San Juan Co., N. M. (Knowlton, F. H., U. S. Geol. Surv. Prof. Paper 98: *pl. 84, fig. 3.* 1916).

Anemia occidentalis Knowlton—

Raton formation, Paleocene: Trinidad, Colo., Yankee, N. M. (Knowlton, F. H., U. S. Geol. Surv. Prof. Paper 101: *pl. 54, fig. 2.* 1917).

Anemia supercretacea Hollick—

Vermejo formation, Upper Cretaceous: Rockvale, Colo. (Knowlton, F. H., U. S. Geol. Surv. Prof. Paper 101: *pl. 30, fig. 5.* 1917).

It is thus clear that the family Schizaeaceae, and particularly the genus *Anemia*, once enjoyed a much more northerly distribution than at present. *Anemia* is now confined to the American tropics and subtropics (with the exception of one species from South Africa), extending northward only into the southern part of the United States.

Anemia sp.

Fragments of fronds have been found at a number of points along the outcrop, which are closely comparable with certain living species of *Anemia*. Although similar in certain respects to *A. Fremonti* they are much less robust and have not been found associated with the fertile pinnae of the latter.

The most complete specimens that we have discovered are shown in figs. 30–32, 34. Those shown in the first two figures probably represent nearly complete fronds which are characterized by a rather long slender stalk, twice pinnate, with a tendency toward a tertiary division in the basal pinnae (fig. 31). It is quite possible that these fronds are simply small specimens of *A. Fremonti* but since they have not been found closely associated with that species it seems best to describe them separately. There is, moreover, a striking similarity to the Wealden fern, *Ruffordia Goepperti*, which Seward ('94) likewise includes in the Schizaeaceae.

GLEICHENIACEAE

Gleichenites coloradensis (Knowlton) Andrews, n. comb.

Dryopteris coloradensis Knowlton, U. S. Geol. Surv. Prof. Paper 108-F: 83, *pl. 30, figs. 3, 4.* 1917.

This apparent fern was included by Knowlton in the Polypodiaceae, a justifiable conclusion considering the fragments of foliage that he had available for study. Although our specimens do not bear reproductive structures, a considerable amount of information has been obtained concerning the structure of the frond as a whole. As may be judged from the following description, it is strikingly similar vegetatively to certain species of *Gleichenia,* the resemblance being sufficiently great to warrant its transference from *Dryopteris* to the genus *Gleichenites* of Goeppert.

Collections were made at three localities along the plant-bearing outcrop, at points approximately 1½, 1¾ and 2 miles north of Little Muddy Creek. Most of our material came from the last two localities where it occurred as a "pure stand," there being no other associated fossil plants.

Knowlton did recognize that it was a plant of considerable size. He writes, "From the presence of large pieces of stems intermingled with the fronds and presumed to belong to them, it is assumed that this fern was probably of large size, but the direct evidence is only sufficient to say that it is at least bipinnatifid." In all probability the "large pieces of stems" that Knowlton mentions are fragments of the rachis. The most distinctive feature of the frond lies in its successive trichotomous-like branchings. The rachis is of considerable size, as may be noted in figs. 20 and 26, a number of fragments similar to that shown in fig. 26 having been found. The central member of the "trichotomy" may grow out (fig. 20) or remain abortive (figs. 21, 24), but it does seem to have been more generally developed in the fossil than in living species such as *Gleichenia pectinata*.

In the reconstruction of the frond in fig. 21 it has been assumed that *c* corresponds to the primary subdivisions of the specimens shown in figs. 20 and 26. The specimen shows three

further divisions, the last of which lies on the counterpart of the specimen and is shown at *b*, fig. 22 (the negative has been reversed so as to show it in the same orientation as fig. 21). The pinnules are arranged on the ultimate (fourth order) subdivisions as shown in figs. 24, 27. Figure 29 has been included to show more clearly the typical pinnule morphology.

The removal of this species from the genus *Dryopteris* seems fully justifiable in view of our present knowledge of the structure of the frond. Had Knowlton had more complete specimens he would undoubtedly have placed it in the Gleicheniaceae. Because of the fact that sporangia still remain to be discovered it seems best to refer the plant to *Gleichenites*.

Of the various species of *Gleichenites* that have been described (Hirmer, '27, pp. 623–4), *G. coloradensis* compares most closely with *G. Gieseckiana* Heer. The characteristic mode of branching, as well as the morphology of the pinnules, is very similar to specimens of the latter described by Seward ('26) from the Cretaceous of Greenland. It was apparently a widespread species during Cretaceous times, specimens having been reported from Spitsbergen, England, France, Germany, Russia, Sakhalin (Japan), Dakota and New Jersey (Seward, '26, p. 147). In view of this circumpolar distribution of *G. Gieseckiana*, it is not surprising to find the very similar, if not identical, *G. coloradensis* in the Upper Cretaceous of southwestern Wyoming.

Where reconstructions of fossil plants or parts thereof can be prepared with a reasonable degree of accuracy it seems desirable that the plant be presented in that fashion. The figured specimens, as well as numerous others from which information has been drawn, bear out the accuracy of our restoration of the frond as we believe it appeared in life (fig. 41). Whether or not the entire frond is represented is, of course, not certain. As our material indicates but four orders of branching, only that many have been shown, and since no rachis fragments larger than those shown in figs. 20 and 26 have been found it is likely that the entire frond is represented. Some of the terminal branches have been eliminated in the restoration in

order that the structure of the terminal pinnae might be brought out more clearly.

The distinctive morphology of the fronds, as well as the sori and sporangia of *Gleichenia,* has enabled its scattered fossil remains to be assembled into one of the most interesting stories of geographical distribution presented by an extant genus. Confined now to the tropics and sub-tropics, *Gleichenia* once enjoyed a range far north of its present confines. It has been described from Jurassic and Cretaceous rocks of Greenland, and from the Cretaceous period numerous localities in North America, to mention a few: Maryland, New Jersey, Kansas, Colorado, Wyoming, California, British Columbia.

In 1935 Seward wrote, "The sight of well preserved fronds of Ferns with forked arms exposed on a slab of shale on the beach of Upernivik Island (71° N. lat.) took me back to a hill-side above Penang in the Malay Peninsula, where living Gleichenias in company with *Dipteris* formed a wonderful tangled carpet of luxuriant growth on the edge of a tropical forest." No more striking contrast to either the arctic or tropical climates could be found than the present semi-desert sage-brush hills of southwestern Wyoming whose climate must have been much more like that of Penang in Upper Cretaceous times than it is at present.

CYATHEACEAE-DICKSONIACEAE

Microtaenia Knowlton

In his account of the Frontier flora Knowlton described two species under this genus, *M. variabilis* and *M. paucifolia* (Hall). In both cases apparently fertile fronds were described and figured but no actual evidence of their fertility was given. As we have succeeded in isolating spores from both species a further account of these interesting ferns is presented here.

Microtaenia paucifolia (Hall) Knowlton, U. S. Geol. Surv. Prof. Paper 108-F: 82–83, *pl. 30, figs. 1, 2.* 1917.

Fertile fragments of this species were found to be fairly abundant, particularly within a radius of ½ mile to the north and south of Little Muddy Creek. The greatest part of the

fragments apparently had matured previous to fossilization since of the numerous ones collected only two have yielded spores. The largest specimen (fig. 16) was deposited before spore dispersal as spores have been found in all of the sori studied. When the large globose bodies terminating the pinnules were removed from the rock and macerated in nitric acid and potassium chlorate for a few minutes, a residue of spores resulted (fig. 17). The triradiate commissure is clearly shown. The exine is rather delicate and smooth, with no evidence of sculpturing of any sort. All the spores are distinctly triangular as shown in the figure, and although this may be due in part to collapse it may represent the actual shape of the spore in life. There is very little variation in spore size, all being about 26 μ in diameter.

No evidences of sporangia have been found in the globose terminal supposed sori. There remains the possibility that the "sori" are actually single terminal sporangia. There is a striking resemblance of these structures to the Jurassic genus *Coniopteris*, particularly of *C. hymenophylloides* (see Thomas, '11, *pl. 3, figs. 1, 4, 5;* Seward, '00, *pl. 17, fig. 8*). However, no foliage has been found in the Frontier formation which compares at all closely with that of *Coniopteris*. Because of the close similarity between *Microtaenia paucifolia* and the fertile pinnae of *Coniopteris hymenophylloides,* which is generally accepted as being referable to the Dicksoniaceae, it seems advisable to include *Microtaenia* within that family instead of the Polypodiaceae following Knowlton's classification.

Microtaenia variabilis Knowlton

Only two fertile fragments of this plant are included in our collection. Figure 13 shows one of these magnified nearly 5 times and fig. 14 is a portion magnified 24 times. It differs from *M. paucifolia* in the broader, more leaf-like nature of the pinnae. In fig. 14 a single vein may be seen passing out to each sorus.

Sporangia have not been observed but a few spores have been obtained. Their walls are delicate and wrinkled (fig. 15)

and there is no evidence of sculpturing or a triradiate commissure.

<div align="center">EQUISETACEAE</div>

Equisetum sp.

In his report on the Frontier plants Knowlton described and figured a species of *Equisetum* based on a supposed underground stem. In our collection of the past summer we have a specimen referable to his species, but it is far from being a convincing representative of the genus. Other specimens have been found, however, of a much less doubtful nature. A nodal diaphragm is shown in fig. 18. This was associated with rather poorly preserved stem fragments which, although a specific name would be meaningless, does attest to the presence of the genus in the flora.

<div align="center">PLANTAE INCERTAE SEDIS</div>

Baiera sp. (?)

The problematical specimens described under this name were found at only one locality, about 1½ miles north of Little Muddy Creek. The most complete specimen that was collected is shown in fig. 28. It may be noted that this dichotomizes five times and, as in the other specimens illustrated (figs. 19, 23, 25), the branching is equal or nearly so in all cases.

In the right-hand primary fork of the specimen shown in fig. 28 a single vein may be discerned in each subdivision. The vein divides some distance before reaching the dichotomy of the lamina (this term is employed on the assumption that the fossil does represent a leaf of the *Baiera* type). Unfortunately, the fossils are preserved in a coarse sandy shale, there being no cuticular remains.

There is a close superficial similarity between our specimens and certain species of *Baiera*, particularly *B. spectabilis* (Walton, '40, *fig. 124a*) and a specimen tentatively referred by Seward to *B. Lindleyana* (Seward, '26, *pl. 10, fig. 101*). There are, however, other possibilities that merit consideration.

In 1895 Seward described, under the name of *Becklesia anomala*, a fossil plant from the Wealden of England, consist-

ing of a central axis with pinnately arranged branches which in some cases "appear to bifurcate close to the point of attachment to the central axis." He compared his specimen with the peculiar forked leaflets of the living *Macrozamia heteromera* Moore. A study of herbarium specimens of the latter revealed a rather striking similarity although the Frontier fossils are somewhat larger and appear to have been more laxly disposed.

Summary

The preceding is an account of certain fossil plants from the Upper Cretaceous Frontier formation of Wyoming. Well-preserved compressions of fertile pinnae of a schizaeaceous fern are described and shown to be referable to *Anemia Fremonti* Knowlton. Since the sterile and fertile parts of the frond have not been found in actual organic connection the latter are described as forma *fertilis*.

Fronds of the supposed polypodiaceous fern *Dryopteris coloradensis* Knowlton are shown to possess vegetative characters distinctive of *Gleichenia* and are redescribed as *Gleichenites coloradensis*.

Spores have been obtained from the fertile fronds of *Microtaenia variabilis* Knowlton and *M. paucifolia* (Hall) Knowlton.

The presence of *Equisetum* in the flora is recorded and fossils referable to *Baiera* are described.

Acknowledgment

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EXPLANATION OF PLATE

### PLATE 1

Anemia Fremonti Knowlton forma *fertilis* Andrews.

Fig. 1. Two primary branches of fertile pinna. Photograph from a nitro-cellulose transfer. No. 1312, × 4.

Fig. 2. Primary branch of fertile pinna. Only one pinnule cluster is shown on each secondary branch, the others having been removed with the counterpart, lost prior to fossilization, or are deeply imbedded in the matrix. No. 1309, × 3.3.

Fig. 3. A nearly complete young fertile pinna. No. 1313, × 3.

Fig. 4. Primary branch of a somewhat older fertile pinna, as evidenced by its greater size and more expanded condition of the pinnule clusters. Two of the latter may be clearly distinguished on most of the secondary branches. No. 826, × 3.2.

Fig. 5. Primary branch of a fertile pinna. Photograph from a nitrocellulose transfer. No. 1311, × 4.
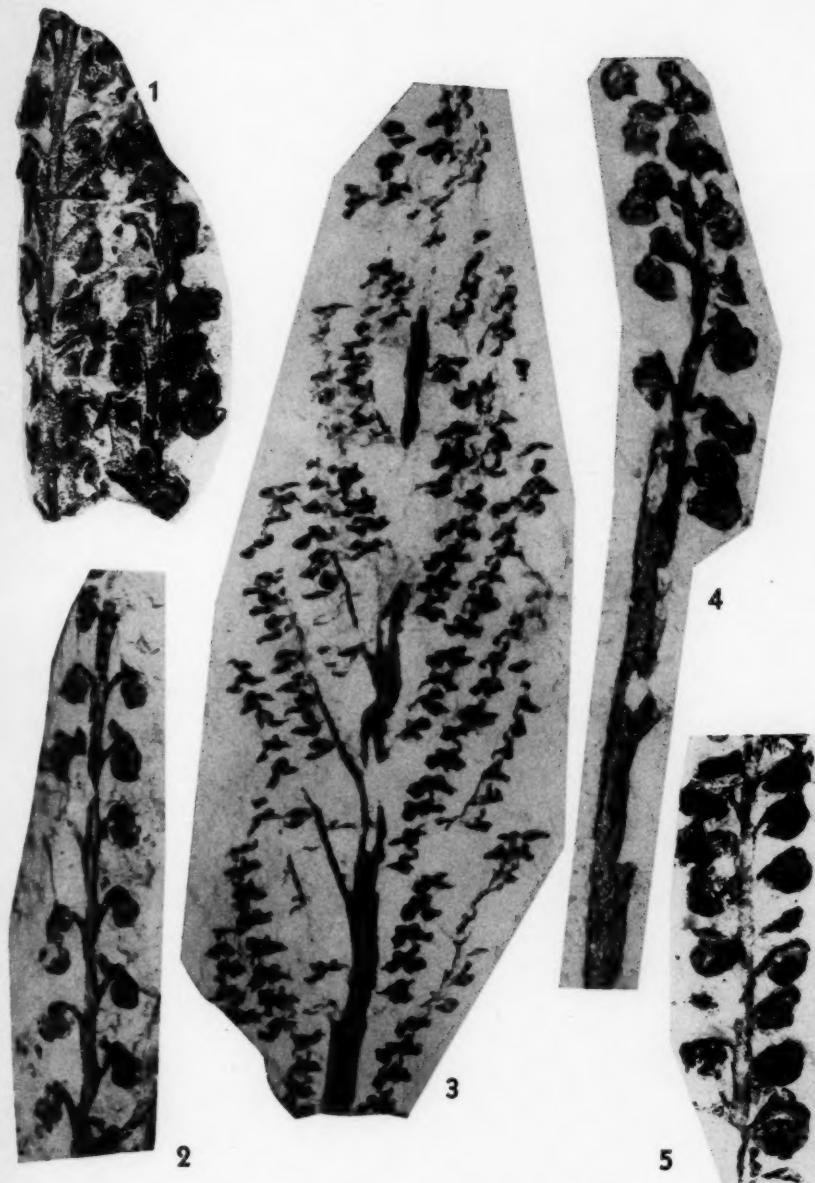
PLATE 1

ANDREWS & PEARSALL—FLORA OF FRONTIER FORMATION
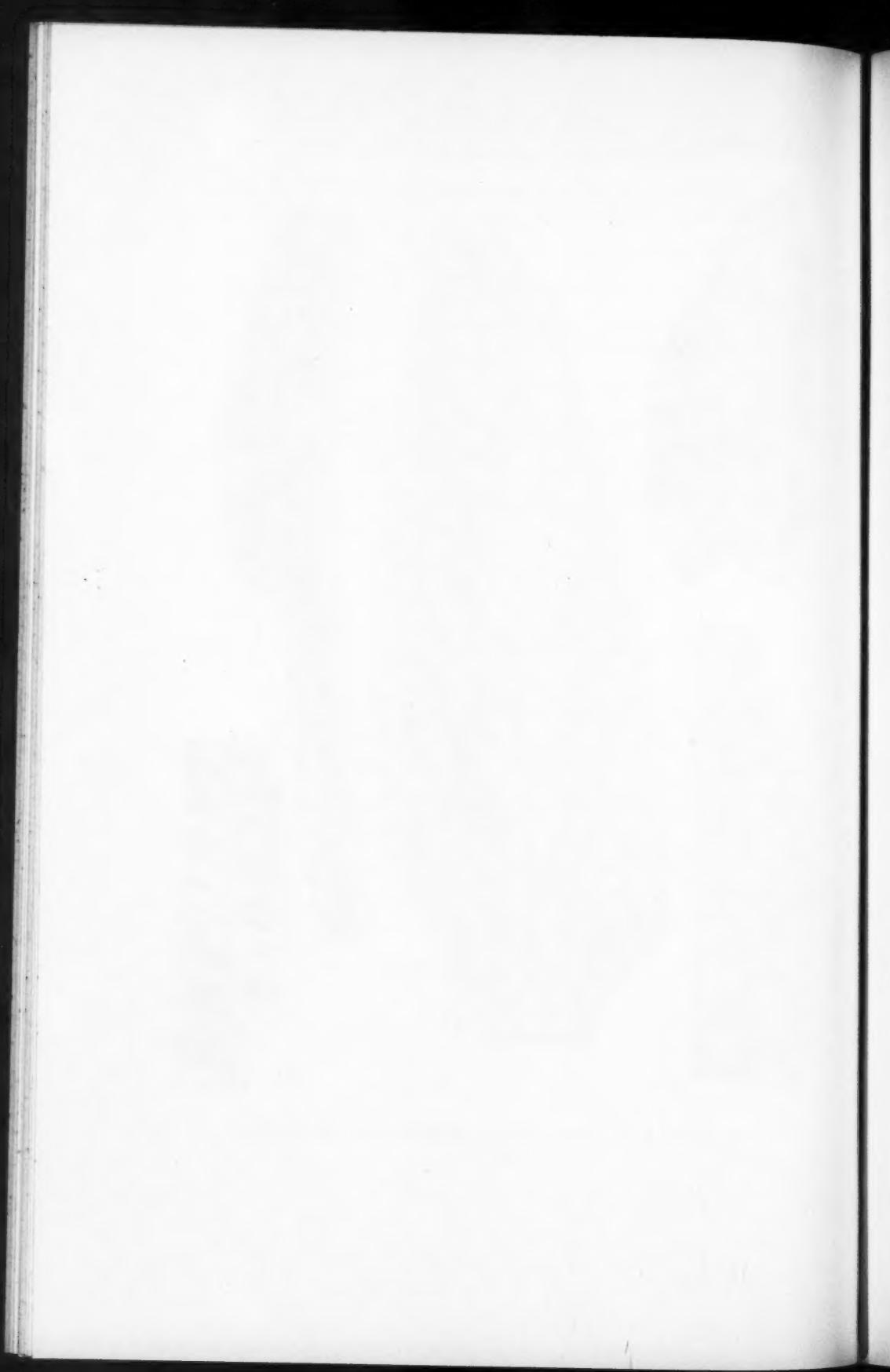
EXPLANATION OF PLATE

PLATE 2

Figs. 6–12. Spores of *Anemia Fremonti* forma *fertilis*. Figs. 7 and 8 are of opposite sides of the same spore. Fig. 12 is of a tetrad, all × 750.

Figs. 13–15. *Microtaenia variabilis* Knowlton. Fig. 13. Portion of fertile frond. No. 1308, × 4.8. Fig. 14. Portion of same more highly magnified, × 24. Fig. 15. Spore, × 750.

Fig. 16. *Microtaenia paucifolia* Knowlton. Portion of fertile frond showing the large, terminal, globose sori (or sporangia?). No. 1310, × 1.7.

Fig. 17. Spore of same, × 750.

Fig. 18. *Equisetum* sp. nodal diaphragm, × 2.3.
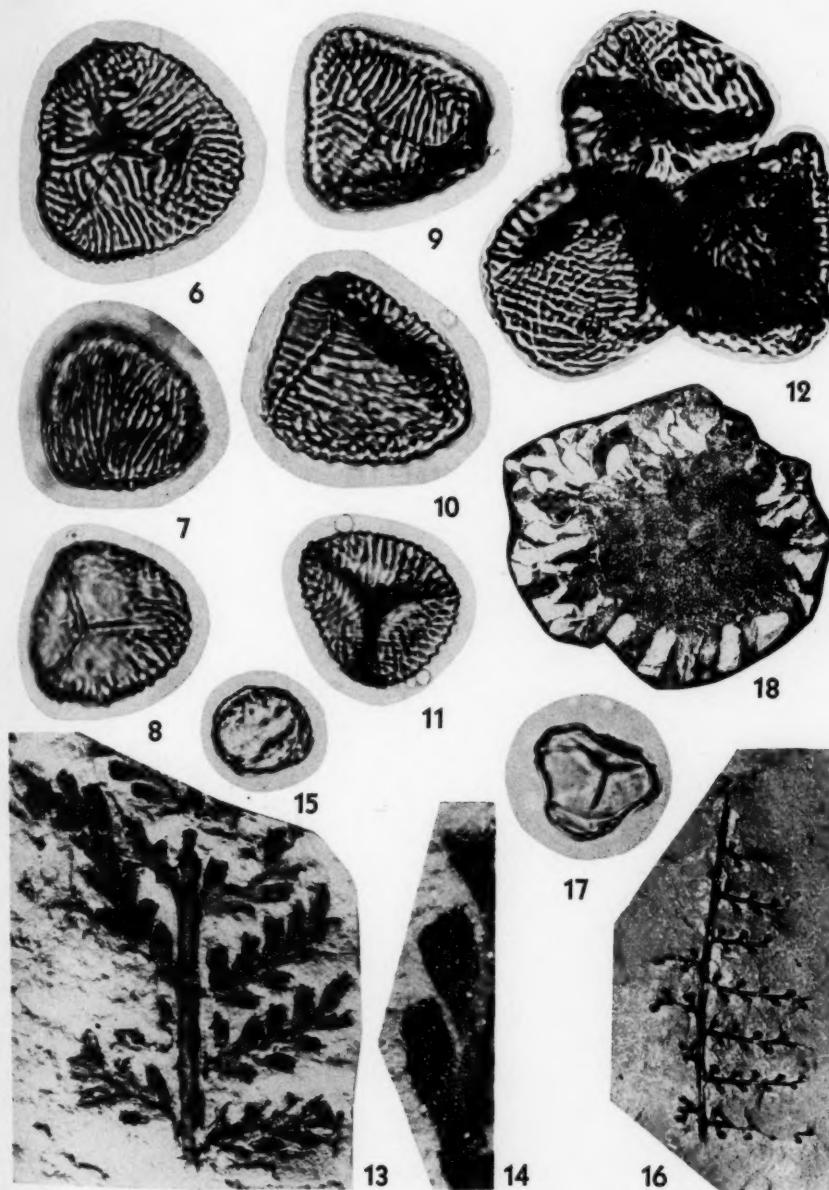
PLATE 2

ANDREWS & PEARSALL—FLORA OF FRONTIER FORMATION
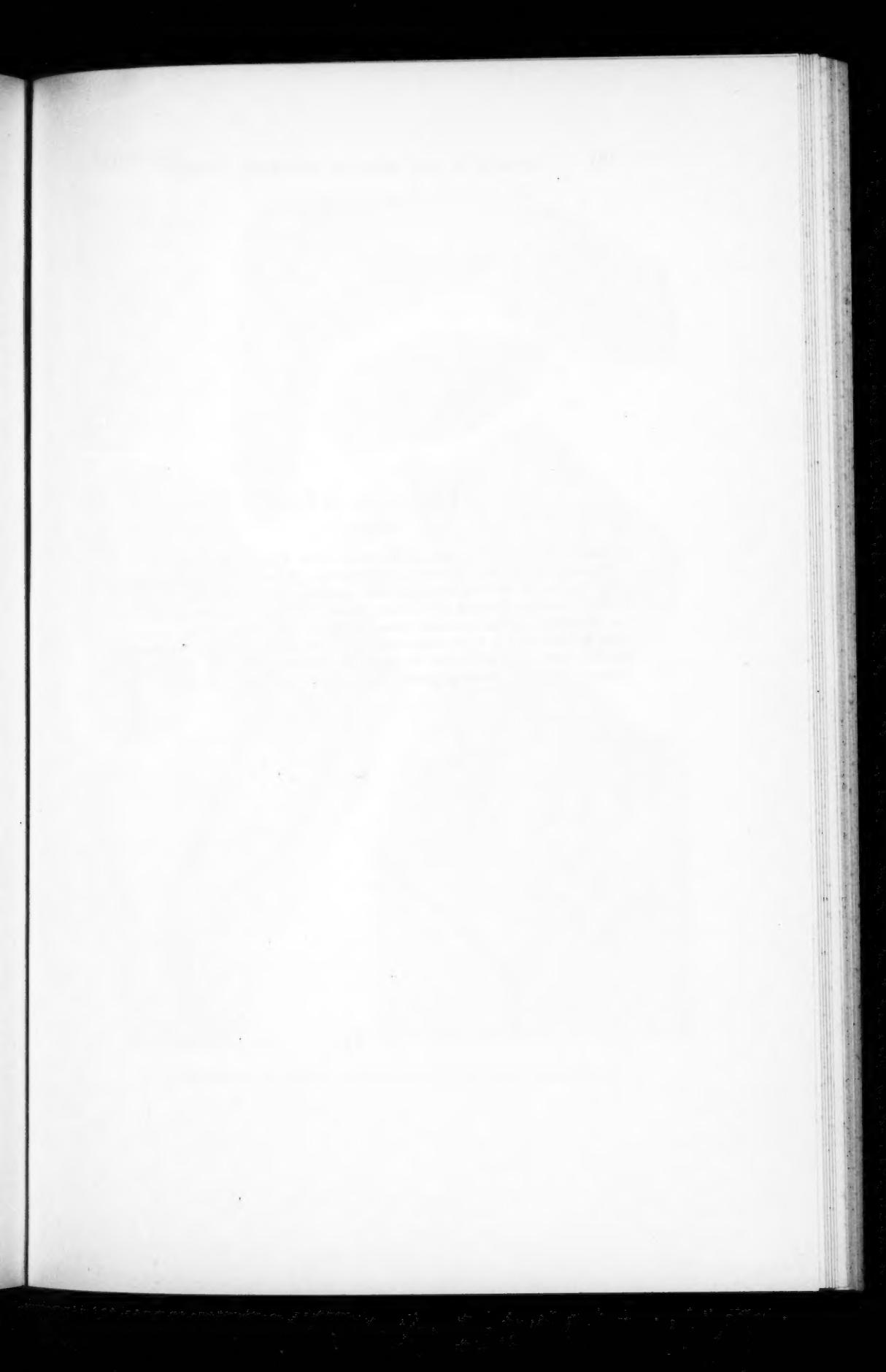
EXPLANATION OF PLATE

PLATE 3

Figs. 19, 23. *Baiera* sp. Fig. 19. No. 1302, × 1.3. Fig. 23. No. 1301, × 1.

Figs. 20, 21, 22, 24. *Gleichenites coloradensis* (Knowlton) Andrews. Fig. 20. Basal portion of frond showing primary branching. No. 1296. Fig. 21. Portion of frond showing secondary and tertiary branch. No. 1293. Fig. 22. Photograph of the counterpart of the specimen shown in fig. 21. The negative was reversed in order to show the two in the same orientation. No. 1294. Fig. 22a corresponds to fig. 21a, while the fourth order of branching is shown at fig. 22b. Fig. 24. Final (fourth) branching showing pinnule morphology. No. 1298. All approx. × .8.

PLATE 3

ANDREWS & PEARSALL—FLORA OF FRONTIER FORMATION

EXPLANATION OF PLATE

PLATE 4

Figs. 25, 28. *Baiera* sp. Fig. 25. No. 1304, × 1. Fig. 28. No. 1303, × 1.4.
Figs. 26, 27, 29. *Gleichenites coloradensis*. Fig. 26. Primary branching of frond.
No. 1292, × 1. Fig. 27. Fourth order of branching. No. 1291, × 1. Fig. 29. Portion of a terminal branch showing pinnule morphology. No. 1297, × .9.
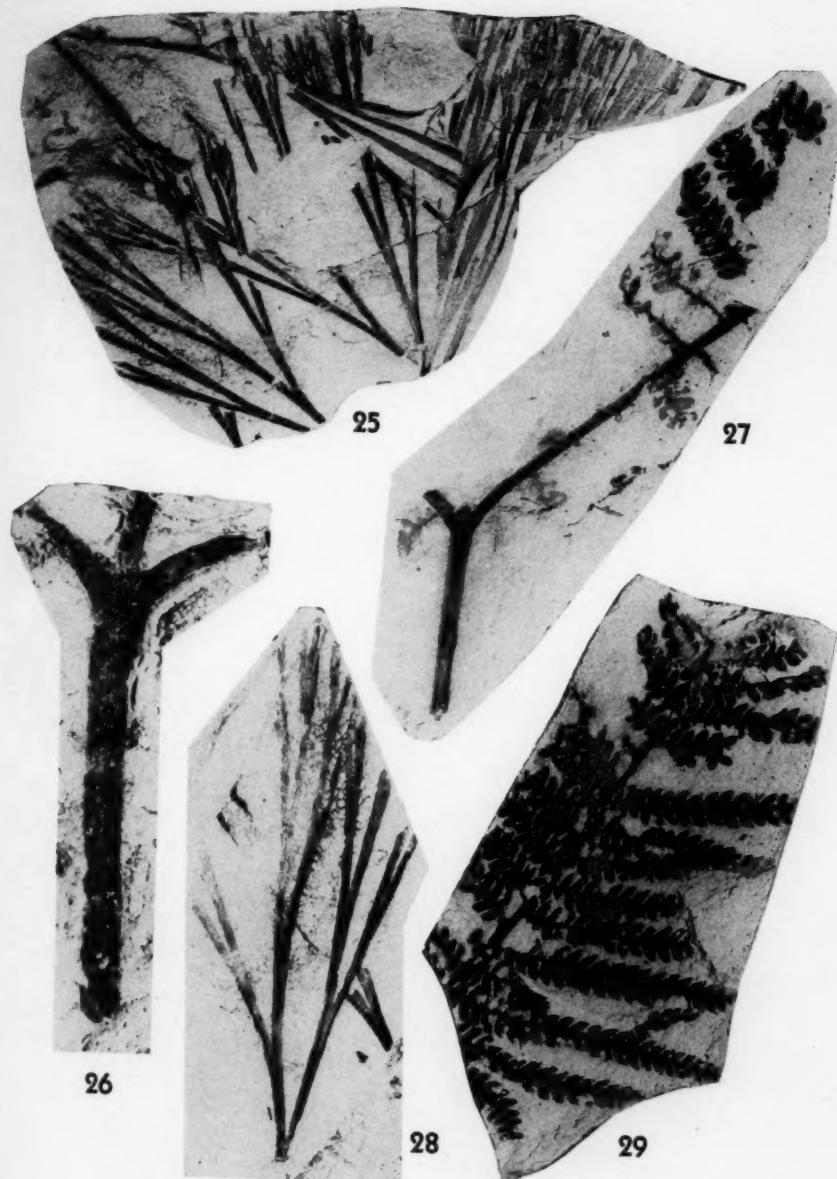
ANDREWS & PEARSALL—FLORA OF FRONTIER FORMATION
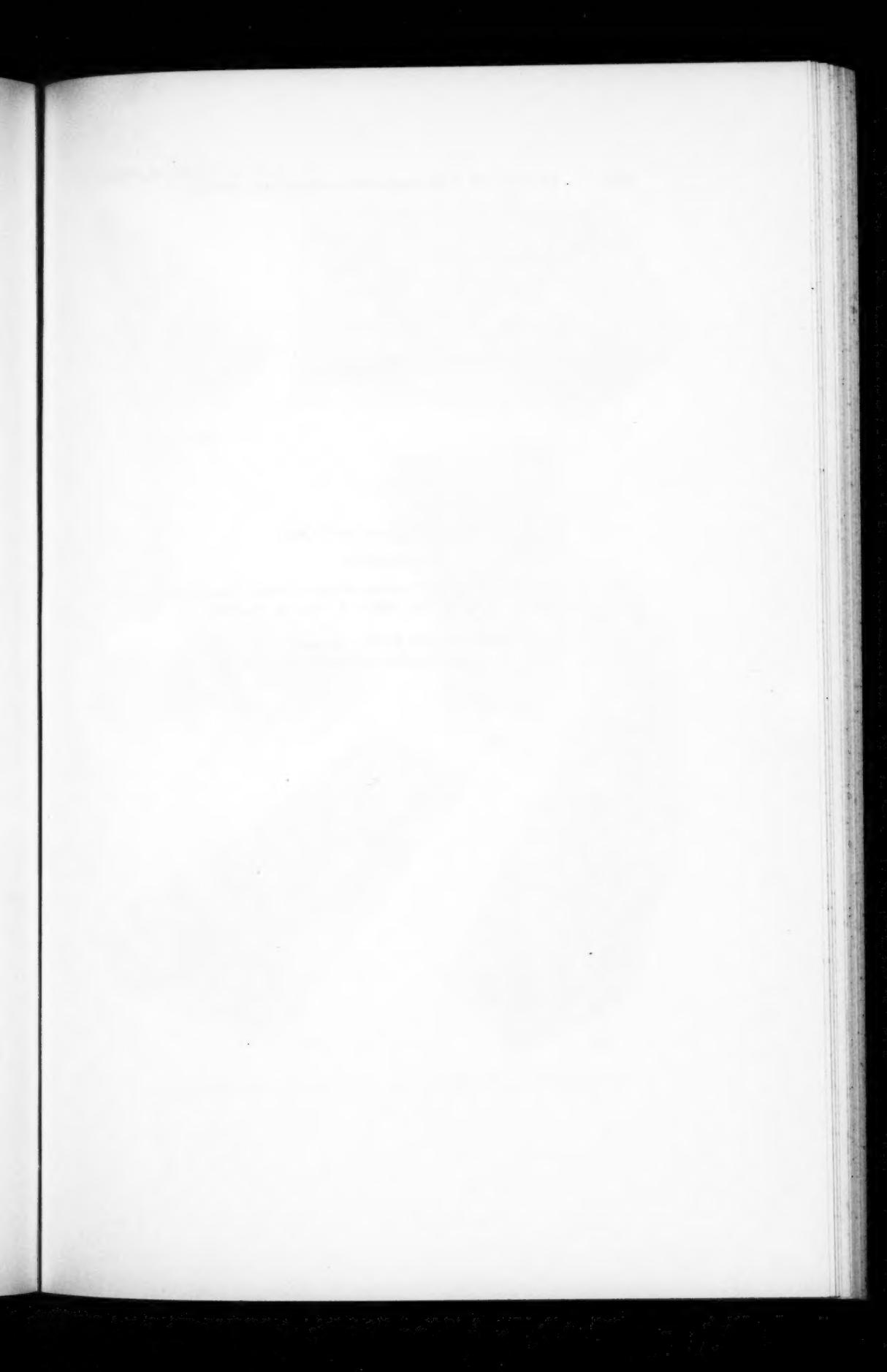
EXPLANATION OF PLATE

PLATE 5

Figs. 30, 31, 32, 34. *Anemia* sp. Portions of sterile fronds. Explanation in text. Fig. 30. No. 1300, × 1. Fig. 31. No. 1299, × 1. Fig. 32. No. 1307, × 1. Fig. 34. No. 1295, × .9.

Fig. 33. *Anemia Fremonti* forma *fertilis*. Annulus, × 160.

Fig. 35. *Anemia Fremonti*. Terminal portion of frond. No. 1305, × 1.
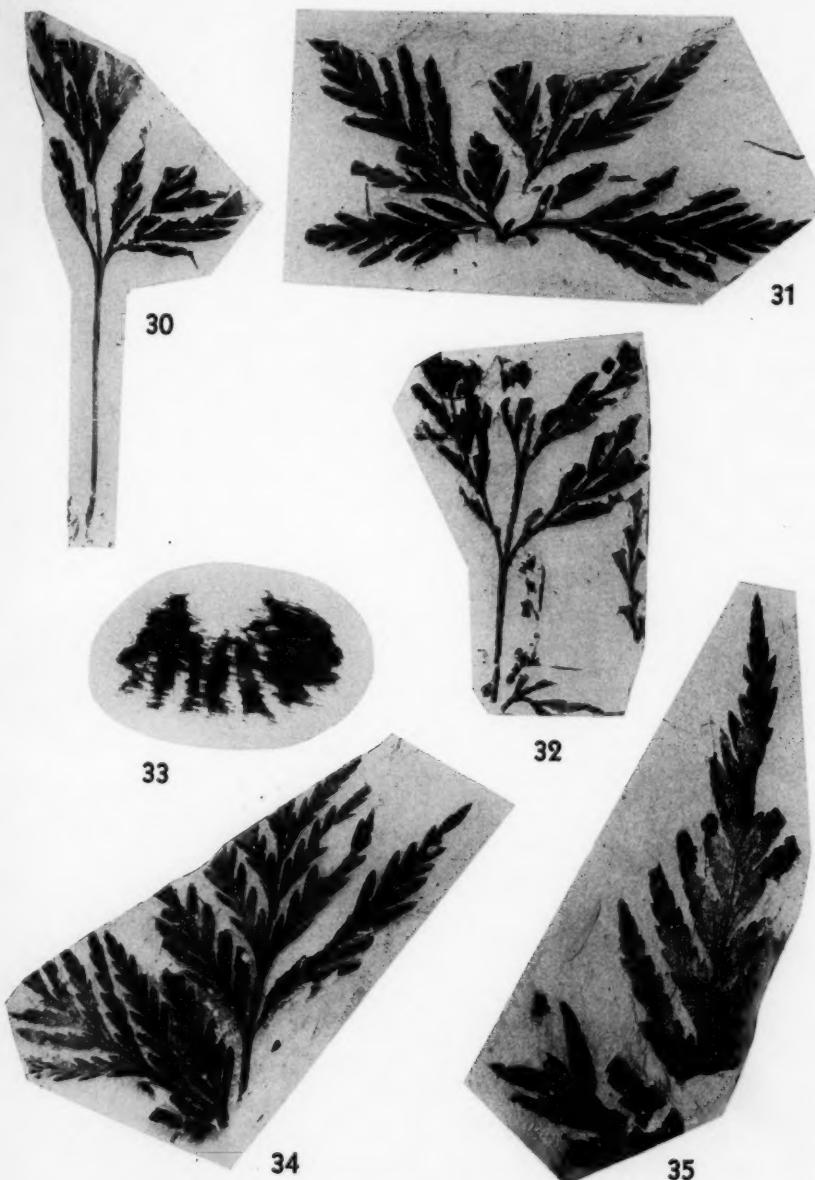
Plate 5

ANDREWS & PEARSALL—FLORA OF FRONTIER FORMATION
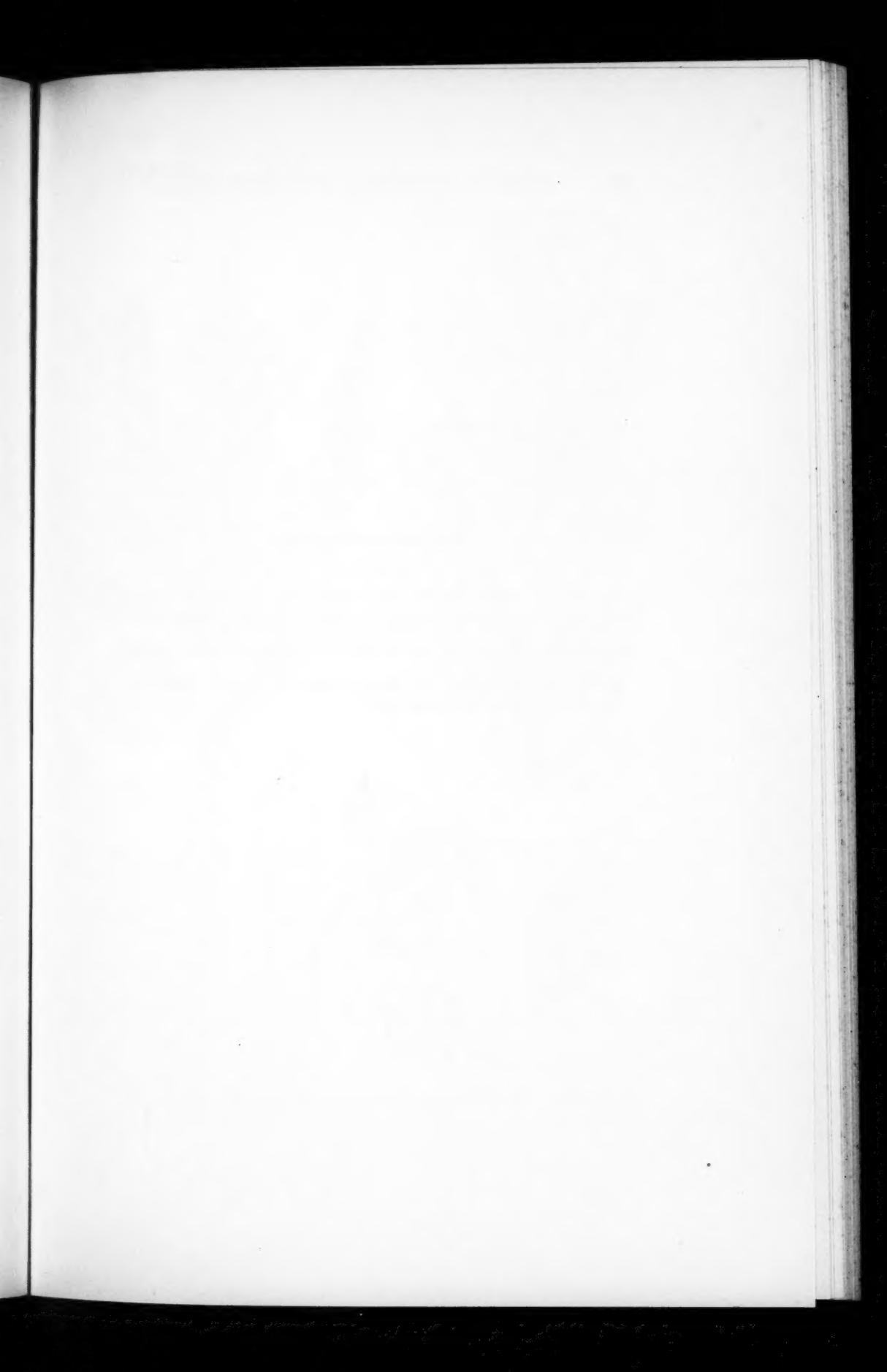
Explanation of Plate

PLATE 6

Figs. 36–38. *Anemia Fremonti* forma *fertilis*. Fig. 36. Portion of primary branch of a fertile pinna showing a secondary branch after treatment with macerating fluid, × 15. Fig. 37. A single pinnule cluster in side view showing the sporangia arranged in two rows along the under-surface of the pinnules, × 30. Fig. 38. Undersurface of a single pinnule, × 30.

Fig. 39. *Anemia Fremonti*. Part of sterile portion of frond. No. 1306, × 1.

Fig. 40. Restoration of complete frond.

PLATE 6

ANDREWS & PEARSALL—FLORA OF FRONTIER FORMATION

EXPLANATION OF PLATE

PLATE 7

Fig. 41. Restoration of frond of *Gleichenites coloradensis.*

Plate 7
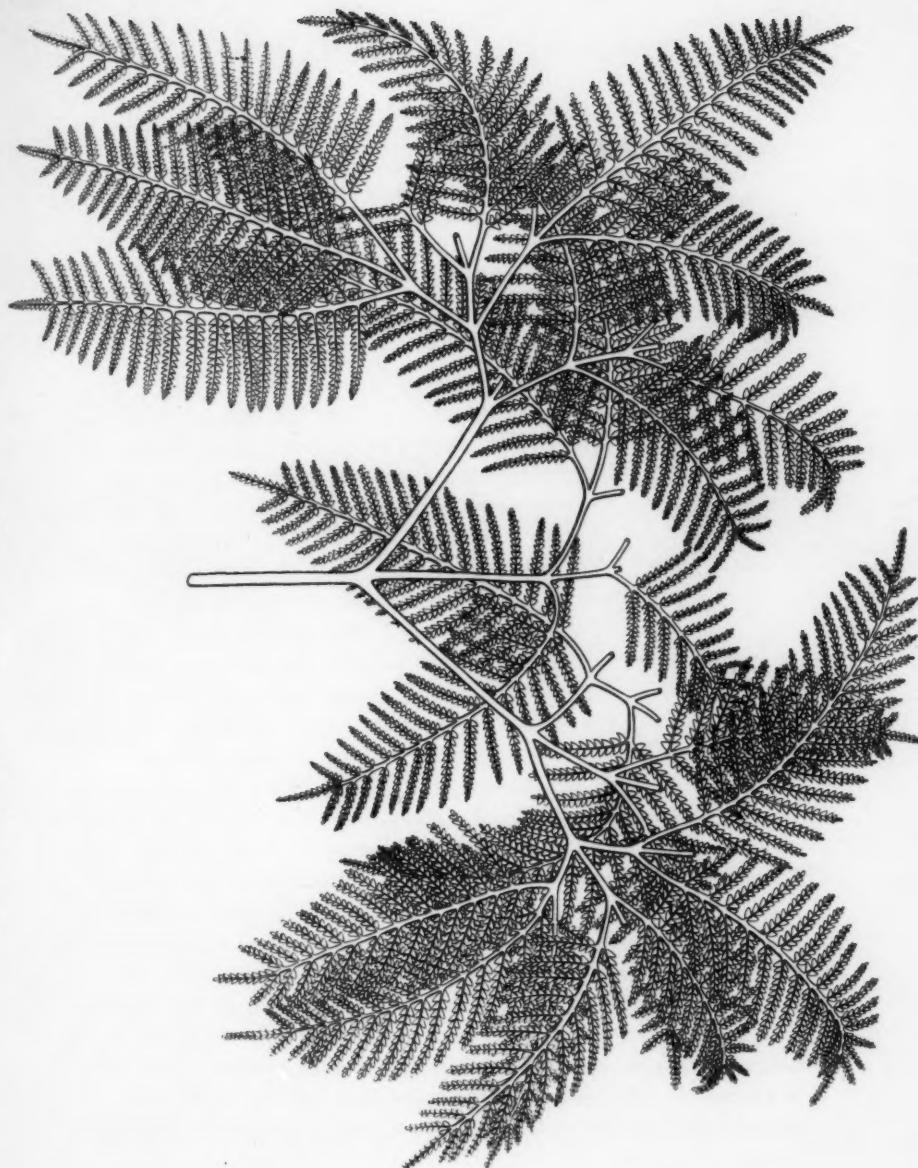
THE NORTH AMERICAN ASCLEPIADACEAE

I. Perspective of the Genera

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Introduction

The problem of the North American genera of Asclepiada-ceae has been summarized well by Standley (Fl. Costa Rica 3: 949. 1938): "The family is noteworthy for the complicated structure of the flowers, more complicated, probably, than those of any other family of plants. The Mexican and Central American members of the group have never been monographed properly, and their classification is at present in a decidedly chaotic state."

It is unfortunate that Charles Darwin did not compose a study on the floral structure and pollination of Asclepiads as a companion to his famous observations on Orchids. In both groups, as distantly related as Dicotyledons and Monocoty-ledons may be, entomophily has produced elaborate and vari-able innovations from group to group. But apparently with the same intention: for the attraction of insects and cross-fecundation by them, through means of a pollinium.

The Orchids have responded to entomophily largely by zygomorphy and elaboration of the perianth. In the Ascle-piads, on the other hand, actinomorphy has been retained, and, although corolline modifications are obvious, diversification is due chiefly to the structural plasticity of the staminal fila-ments. These elaborations of the stamens are known as the corona. Since the anthers of Asclepiads are invariably five in number, it obtains that the corona also is five-parted, the seg-ments being quite free or mutually coherent, and diversified in ways that are too numerous for description. Although a staminal corona is the rule for the group, a few entities possess

simple filaments. In any event, the center of the flower is occupied by a composite structure known as the gynostegium, comparable to the column of Orchids. This consists of the five coherent stamens surrounding the style of the bicarpellate pistil, with an enlarged terminal "stigma head" at the free end. The whole stigma head is not truly stigmatic, the receptive surfaces being five narrow strips of glandular tissue between the contiguous anthers.

The anthers of American Asclepiads are bilocular, and within each cavity the pollen grains are grouped at maturity into a glutinous, sac-shaped pollinium of definite form and size. In the subfamily Cynanchoideae, containing all the New World species, these pollinia are combined by pairs through a more or less elaborate yoke mechanism called the translator. The translators consist of two arms* attached to their respective pollinia, and are themselves joined by a roughly sagittate body called the "gland."* A pair of pollinia, therefore, consists of the contents of adjacent anther cavities of contiguous anthers. The translators, with their glands, are formed between the neighboring anthers.

The current explanation of the formation of the translators is that their substance consists of the solidified secretion of special glandular cells located upon the stigma head. Investigations of my own, not yet completed, lead me to assume that in the early development of the pollinia the tapetal liquid, characteristically abundant in young anthers, seeps through small pores of the neighboring anthers to gather in the commissural grooves of the two organs. This liquid later solidifies outside the anther as well as about the pollen, instead of being absorbed as is usually the case. Superficial support is given this view by the fact that the uniting "gland" always is distinctly 2-parted. According to either view, the translators are moulded when still in the liquid state by the available spaces between the young anthers.

* "Translator arm" and "gland" frequently are called "retinaculum" and "corpusculum" respectively in the literature. The former are chosen here as being somewhat more easily associated with the appearance of the structures as well as more adaptable to English: the latter are more useful in Latin diagnoses.

When the pairs of pollinia are mature they are easily re-
moved from the dehiscent anthers by means of the yoke-like
translators. A visiting insect may be observed to pull them
out and carry them away suspended from its legs. On the same
or another flower, the pollinium must be inserted between the
anthers at the stigmatic surface, in order to insure pollination.
At that time, in response to the stigmatic secretions, pollen
tubes germinate from the pollinium while still intact, to travel
down the style to the ovules. The significance of the pollinia
and their method of fecundation were fully appreciated for the
first time by Robert Brown (Mem. Wern. Soc. 1: 12–58. 1809)
in his celebrated paper distinguishing the Asclepiads from the
Apocynads.

The method of pollination in Asclepiads which Robert
Brown disclosed appears at first sight to be of design so cun-
ning that great fecundity of the plants should be assured, as
well as frequent hybridization. Every conceivable innovation
would seem to have been made by the flowers to insure success-
ful insect ministrations. But such does not necessarily seem
to have resulted. The family as a whole is outstanding for the
constancy of its species and the rarity of obvious hybridity.
Furthermore, the amount of fruit produced scarcely seems to
be commensurate with the "efforts" taken to insure it, to speak
anthropocentrically.

Accounts of the pollination of Asclepiads seldom mention
the actual difficulties intervening: the danger of the pollinia
being broken or only partially withdrawn by the insect's casual
visits; the horny margins of the anthers which seclude the
stigma, frequently with entangling hooked or grooved decora-
tions.

Germinated pollinia are conspicuous, even in dried and
boiled material, because of the abundant, felty pollen tubes.
Amongst the hundreds of flowers of various genera and species
which I have dissected under magnification, I have found very
few indeed bearing germinated pollinia in the stigmatic cham-
ber between the anthers. Of those few, the companion pol-
linium was usually in place in its mother anther sac. In nu-

merous instances I have found germinated pollinia while still within the anther sac. Whether such pollen tubes can reach the ovules successfully has not been ascertained, but it is not impossible. Such observations explain to some extent the rarity of hybridization, but fail to shed much light on the use of the pollinia as agents for pollination by insects.

Another feature of the Asclepiad flower which would appear to have little positive survival value is the division of the stigma into five rather restricted receptive regions. This apparently is responsible for the fact that only one follicle commonly develops from the two carpels of the pollinated pistil. Thus, even though three stigmatic surfaces were to receive pollinia, fecundation of only one carpel might result: but it must be confessed that conversely were only two pollinia deposited development of both follicles might ensue. A pair of follicles, nevertheless, is seldom encountered. Perhaps it is safe to assume that the reduction in number of fruits is compensated by the volatility of the comose seeds.

The classification of Asclepiadaceae into major divisions is based upon the nature and position of the pollinia, and thus owes its foundations to the classical observations of Robert Brown (Mem. Wern. Soc. 1: 12–58. 1809). That versatile genius separated the family as it is now recognized into five tribes: Periploceae, with open cornucopia-shaped pollinia and adhesive translators somewhat as in the Orchids; Secamoneae, with 4-locular anthers, the yoke-like translators bearing two pollinia upon each arm; Asclepiadeae Verae, with 2-locular anthers, the yoke-like translators bearing a single pendulous pollinium upon each arm; Gonolobeae, with pollinia similar to those of Asclepiadeae Verae, but horizontal; and Stapelieae, with similar, but erect pollinia. Recent systems (cf. K. Schumann, in Engl. & Prantl, Nat. Pflanzenfam. 4^2: 209. 1895) have divided the family into two subfamilies, Periplocoideae and Cynanchoideae; the latter having four tribes, Asclepiadeae, Secamoneae, Tylophoreae (Stapelieae of Brown), and Gonolobeae. In the New World only the Cynanchoideae are encountered in the native flora, with the three tribes Asclepiadeae, Gonolobeae, and Tylophoreae.

In these studies no attempt will be made to subdivide the tribes into the smaller subdivisions advocated by Schumann, for these are manifestly unnatural. Thus the genus *Sarcostemma* R.Br. (sensu stricto) was placed in the subtribe Cynanchinae of Asclepiadeae by that author (K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. **4²**: 245. 1895), but the two certainly synonymous genera, *Philibertia* HBK. and *Funastrum* Fourn., in the Glossonematinae and the Asclepiadinae respectively (pp. 225, 231. loc. cit.). I am inclined also to ignore Schumann's subtribe Astephaninae, characterized by the absence of a corona, since in all cases which I have observed the absence of a crown is the only character separating species groups of obviously close affinity, notably in the inclusive treatment of *Cynanchum* adopted here. One monotypic genus, *Tylodontia* Griseb. (treated as a division of *Cynanchum* here), Schumann includes in the Astephaninae, but I have observed the presence of definite corona segments in an isotype deposited in the herbarium of the Missouri Botanical Garden *(Wright 2964)*. Neither can Oxypetalinae of Schumann be maintained by the appendages of the translator arms, since several South American species of the single genus, *Oxypetalum,* do not have those structures.

The separation of the American Asclepiads into tribes sometimes is a bit difficult, since the position of the pollinia usually must be observed while they are still within the anther sac. Once withdrawn and placed upon the dissecting stage, the delicate translator arms are apt to twist into any conceivable attitude, frequently giving a false impression of their natural position. The Asclepiadeae and Tylophoreae usually are quite easy to detect; but the Gonolobeae have given trouble from the start. I am willing to be convinced that the normal position of the Gonoloboid pollinium may be truly horizontal, although my interpretation of the tribe includes forms with pollinia that range in position from pendulous to ascending. By far the best means that I have found to separate this tribe is by means of the structure, not the position, of the pollinia.

In all the Asclepiadeae and Tylophoreae examined by me, the faces of the pollinium are uniformly rounded or flattened on

either side, and the translator arm makes a sharply definite connection with them. In the Gonolobeae, on the other hand, the faces of the pollinium are more or less dissimilar: one convex or rounded and the other flattened or somewhat excavated, frequently very strikingly so. In some cases both sides are deeply furrowed or excavated. In the Gonolobeae, also, the translator arm usually engages the pollinium more gradually, the attachment being marked by a more or less conspicuous hyaline indentation or margin (always the upper). Without the use of this structural criterion, Schumann placed such genera as *Macroscepis* and *Fischeria* in the Asclepiadeae and *Metalepis* in the Gonolobeae, whereas other characters of the plants show their natural positions to be exactly the reverse, as shall be explained presently.

At this writing ninety-seven genera of Asclepiadaceae have been described from North America, based wholly or in large part upon the structure of the corona. Authors of the great majority of these genera seem not to have understood what a versatile feature this organ is, for it is only when its multifarious aspects are interpreted in a broad and comparative manner that a natural and conveniently referable classification can result. North American students of tropical Asclepiads, particularly, would do well to consider the floral variability of the native Milkweeds before attempting the description of exotic genera. The prospective Asclepiadologist should understand from the first that differences of the corona separate species in this family, which would form remarkable generic criteria, say of the "disc" in other families. After the first shock of surprise at the few genera recognized for North America, readers of the following key to genera may notice the fairly incidental use of corona characters. These are reserved chiefly for subgeneric and sectional distinctions, and will be discussed in that connection.

The term "corona" has been taken in a rather restricted sense in these studies. Amongst earlier literature frequent mention is made of "double" or even of "triple" coronas. This terminology is very confusing except to the authors concerned. Morphologically, the corona, as interpreted here,

consists of various elaborations or enations of the staminal
filaments only. These enations may occur as separate bodies
attached to the staminal column, as in *Asclepias,* to cite a famil-
iar example, or may consist of a more or less entire ring of tis-
sue adnate to the bases of both staminal column and corolla
throat. Where "double" or "triple" coronas have been de-
scribed by various authors, these usually will be found to con-
sist of a faucal annulus of the corolla tube, or sterile append-
ages of the anthers, which are rather to be called such than to
be referred to as corona.

The most cogent reason for avoiding the use of "corona,"
except in a simple sense, is that many readers of the literature
are apt to interpret a corona as double, whilst the author may
not intend such a view. Several instances of possible or pub-
lished confusion arising from an author's use of "double
corona" come to mind. In the subgenus *Chthamalia* of
Matelea, for example, the corona consists of an annular struc-
ture of five more or less united and variously constituted seg-
ments, each of which bears internally a more or less conspicu-
ous ligular process, sometimes surpassing the height of the
subtending segment. Contrary to what one might suppose,
this complex structure is not considered by the literature as a
"double corona." The flowers of *Gonolobus* (sensu stricto)
are very difficult to identify with standard keys, for they
usually possess (1) a faucal annulus of the corolla, (2) a
fleshy, true corona, (3) dorsally appendaged anthers. Some
authors interpret these structures as constituting a "triple"
and some as a "double" corona. Those maintaining the dual
nature may construe either the corolline annulus or the anther
appendages as the supernumerary corona, in which cases the
true corona will be spoken of as either the "inner" or the
"outer" corona, respectively.

The segregate genus *Podostigma,* of the southeastern
United States, is keyed by K. Schumann (in Engl. & Prantl,
Nat. Pflanzenfam. 4^2: 235. 1895) on the basis of having an
"inner corona" borne high upon the column, alternate with the
anthers. When these tiny objects are examined, however, they
are found to be nothing but the minute ligules commonly alter-

nating with the corona hoods in *Asclepias* proper, their normal position doubtless having been disturbed by the elongation of the anther stipe* above the insertion of the hoods. In *Fischeria,* also a "double corona" is described in all texts. But when carefully dissected, the bladder-like "inner corona segments" are found to be nothing but the hypertrophied anthers themselves. This peculiar mark of *Fischeria* may be described more accurately and more clearly upon the basis of anther structure than by introducing an ambiguous and morphologically indefensible reference to supposed "corona."

The North American Asclepiadaceae have never had the attentions of a specialist devoted primarily to their study, except for the period between 1897 and 1904 during which a series of eight short papers by Miss Anna Murray Vail appeared in the 'Bulletin of the Torrey Botanical Club.' These papers consist only of short notes, with the exception of rather casual revisions of *Acerates,* the *Asclepias verticillata* complex, and *Rouliniella* (i.e. *Cynanchum* subgenus *Mellichampia,* in part, of my studies). Even from these small and interrupted beginnings, it is obvious that Miss Vail possessed a very considerable knowledge and insight into the North American Asclepiads, and it is regrettable that her retirement to France terminated her ambitions for more comprehensive works. I must confess that more than once, when I was apparently undergoing swift mental attrition because of the damnably variable coronas and pollinia, I have reflected on my predecessor's retreat to the Riviera.

The South American and Antillean Asclepiads have had several specialists, including Decaisne, Fournier, Schlechter, and Malme; to these must be added the contemporary South American botanists, A. G. Schulz and F. C. Hoehne. The work of these eminent systematists, however, has nearly always been in the field of regional floristics, with few exceptions, such as Malme's monograph and subsequent emendations on *Oxy-*

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* I have found it convenient in dealing with some genera to distinguish two regions of the staminal column: that below the attachment of the corona as the "column," as in most species of *Asclepias* proper, and that above, between the corona and the anthers proper, as the "stipe," as in *Podostigma.*

petalum. But these contributions have affected the northern Asclepiads only in rather minor particulars. Regional floras of North America have included thoughtful interpretations of the Asclepiadaceae in several instances, but have been hindered by their restricted scope and the divided interest of their authors.

Special mention should be made here to the monograph of *Marsdenia* by Rothe (in Engl. Bot. Jahrb. **52:** 354–434. 1915), not only since it is the only comprehensive account of an Asclepiad genus in both American continents, but because the author's solution of the problems of this group closely parallel my own for the family. Confronted by an aggregation of eight segregate genera, nearly all in current use but with very evasive criteria when seen as a whole, Rothe courageously combined them as sections. The result, in spite of some imperfections, is the one bright spot in the determination of tropical American Asclepiads from the existing literature. In the Tylophoreae, at least, one needs no longer to puzzle over the generic interpretation of floral innovations, nor fear that the specimen he is trying to determine may already be described as a new genus in some remote section of the taxonomic indices. At the same time, a natural system of species groups is defined and provided with names which may (or should) be used in the description of novelties, or to which additions may even be made should sufficiently discrepitant plants be found.

A lifetime would be too short to perfect a complete system of the North American Asclepiads. But after an intensive study of several years, I have arrived at a definition of the genera which I believe may well lead to a more adequate understanding of the complex as a whole. The result is a revolutionary change in nomenclature which surely will not be regretted more by the reader than by the author. The change clearly is unavoidable because of the long neglect of the family.

In this group of plants apparent entomophily has produced a floral structure even more complicated and variable than in the Orchids. Morphological details separate species and even varieties here, which would serve to distinguish genera in other groups of Flowering Plants. The student of the Asclepiads is

impelled to the defeatist attitude that only two choices are available in classification: to "lump" genera or to "split" them. If he continues the study of Milkweeds sufficiently long, he probably will find himself tossed from horn to horn of the dilemma.

After several such harrowing experiences, I have recognized that a narrow concept of coronal structure as a criterion of genera, if pursued consistently, will lead to a multitude of monotypic entities—as a matter of fact, that few genera will consist of more than two or three species—and that each new species will introduce anew the question of generic differentiation. This is scarcely an exaggeration when one remembers that an inclusive concept of North American *Asclepias*, alone, involves the listing of twenty generic synonyms. If he contemplates an extended association with the Asclepiadaceae, with yearly increments of specimens brought to his attention for classifying, even the most hardened "liberal" taxonomist will take heed before embarking upon such a disastrous course.

Although the results of my studies wreak havoc upon the existing classification, I feel confident that the groups proposed are natural, and that they will stand the test of many years. The desideratum of stability and convenience will be served much better in having a few, almost infallibly recognizable genera even though they may be large: the natural affinities within these groups may be indicated sufficiently by the erection of subgenera and sections.

This paper is intended as the forerunner of a series devoted to the North American Asclepiadaceae. It is composed as a general survey of the generic elements involved, together with an indication of representative changes in nomenclature made necessary by my visualization of the natural system of the family. These species are drawn only from those with which I am familiar at this time, and should not be considered as complete synopses; neither do they include species not requiring adjustment in terminology. The synonymy, also, is not complete, consisting merely of the name-bringing and other more prominent synonyms. To some readers, the inclusion of the many nomenclatural changes upon such a scanty prepara-

tion may seem precipitate. The decision to include them here, rather than to withhold them for subsequent, complete revisions, has been made in view of the advantages of concrete illustration of the generic elements proposed, the uncertainty of our ability to obtain European types necessary for a complete study within the near future, and the validation of obviously necessary names for the purpose of present determinative work. Should the future permit, this paper will be followed by a monograph of the North American species of *Asclepias*, and by subsequent revisions of the other important genera, in each case with all recognized species illustrated by analytical drawings.

To be of wide use, a critical study of the Asclepiadaceae should be illustrated profusely. I feel that an apology is in order, therefore, because of the total lack of analytical drawings in this paper. Their absence is due in part to the conditions of publication at the moment, and in part to plans which I have made for their inclusion in future studies. After all, this paper is scarcely more than an annotated key to genera, and of little interest save to specialists. Such readers will be sufficiently familiar with the structures to which I call attention not to miss the figures.

Key to the Tribes and Genera

Pollinia strictly pendulous, their faces uniformly flattened or rounded, uniformly fertile to the attachment of the translators........... Asclepiadeae

Pollinia usually horizontal or essentially so, occasionally ascending or descending, but one or both faces more or less excavated, and with a sterile hyaline margin or indentation near the attachment of the translators....Gonolobeae

Pollinia strictly erect, their faces uniformly rounded, uniformly fertile to the attachment of the translators........................... Tylophoreae

Asclepiadeae

Erect or decumbent perennial herbs; pollinia very strongly flattened; corona of 5 cucullate, calceolate, or clavate hoods, usually with an internal horn or crest..I. ASCLEPIAS

Lianas or twining undershrubs; pollinia faces broadly rounded or only slightly compressed.

Arms of translators conspicuously thickened and appendaged near their attachment to the gland.........................II. OXYPETALUM

Arms of translators not as above.
    Corona of 5 separate or united, laminate to filiform scales, oc-
        casionally compounded or with internal processes, rarely wholly
        lacking......................................III. CYNANCHUM
    Corona of 5 semi-vesicular sacs attached separately to the backs of
        the anthers..............................IV. BLEPHARODON
    Corona of 5 closed inflated vesicles joined at the bases by a fleshy
        ring adnate to the corolla-throat..............V. SARCOSTEMMA

GONOLOBEAE

Anthers relatively simple, not conspicuously vesicular, nor with dorsal ap-
    pendages; corolla lobes various, but not crisped............VI. MATELEA
Anthers very conspicuously hypertrophied and vesicular throughout; corolla
    lobes strikingly crisped...............................VII. FISCHERIA
Anthers with spreading, more or less laminate, fleshy dorsal appendages;
    corolla lobes various, but not crisped.................VIII. GONOLOBUS

TYLOPHOREAE

One genus...IX. MARSDENIA

I have been unable to interpret two enigmatic genera of
Baillon, *Microstelma* (Hist. Pl. **10**: 286. 1891) and *Stelmago-
num* (loc. cit. 287), both placed in the Gonolobeae and thus
probably synonymous under *Matelea*.

I. ASCLEPIAS L. Sp. Pl. 214. 1753.

Anthanotis Raf. Fl. Ludov. 52, 149. 1817.
Anantherix Nutt. Gen. N. Am. Pl. **1**: 169. 1818.
Stylandra Nutt. loc. cit. 170. 1818.
Otaria HBK. Nov. Gen. **3**: 192. 1819.
Acerates Ell. Sketch Bot. S. Carol. **1**: 316. 1821.
Podostigma Ell. loc. cit. 326. 1821.
Acerotis Raf. New Fl. N. Am. **1**: 49. 1836.
Oligoron Raf. loc. cit. **4**: 60. 1836.
Otanema Raf. loc. cit. 61. 1836.
Onistis Raf. loc. cit. 63. 1836.
Polyotus Nutt. Trans. Amer. Phil. Soc. n.s. **5**: 199. 1837.
Asclepiodora A.Gray, Proc. Amer. Acad. **12**: 66. 1877.

Schizonotus A.Gray, loc. cit. 1877, non Lindl.
Solanoa Greene, Pittonia **2**: 67. 1890.
Solanoana O.Ktze. Rev. Gen. **2**: 421. 1891.
Oxypteryx Greene, Pittonia **3**: 234. 1897.
Podostemma Greene, loc. cit. 235. 1897.
Biventraria Small, Man. Fl. 1072. 1933.
Asclepiodella Small, loc. cit. 1073. 1933.
Gomphocarpus of American authors.

KEY TO THE SUBGENERA

A. Corolla rotate to rotate-subcampanulate, the lobes reflexed to somewhat
   ascending; corona attached to the column immediately beneath the
   anther head.
   B. Hoods cucullate or cucullate-spatulate to calceolate, rarely strongly
      conduplicate, erect to spreading, the alternate lobules more or less
      deeply 2-cleft, rarely absent.
      C. Corolla throat without internal callous processes.
         D. Hoods usually more or less substipitate as seen from within, the
            basal attachment shallow, conduplicate but not deeply saccate
            ....1. EUASCLEPIAS
         DD. Hoods very sessile, the basal attachment deeply saccate.
            E. Hoods entire to somewhat cleft ventrally, open but occasionally
               appressed against the column.
               F. Base of hoods not appendiculate, or merely somewhat keeled
                  laterally.
                  G. Hoods with a more or less conspicuous internal horn or crest.
                     H. Horn or crest compressed radially; column not deeply sac-
                        cate between the hoods............2. ASCLEPIODELLA
                     HH. Horn or crest compressed tangentially; column deeply
                        saccate between the hoods.........3. PENTASTOMATIA
                  GG. Hoods without a horn or crest.
                     H. Hoods with very pronounced marginal lobes, the orifice
                        not appressed against the column..4. ASCLEPIOPHANES
                     HH. Hoods with very inconspicuous marginal lobes, if any, the
                        orifice appressed against the column......5. ACERATES
               FF. Base of hoods with conspicuous, external, laterally excurrent
                  membranous appendages......................6. POLYOTUS
            EE. Hoods almost completely bifid ventrally, closed, completely en-
               closing the horn if present........................7. SOLANOA
      CC. Corolla with an interrupted faucal annulus of 5 conspicuous callous
         processes alternating with the hoods; hoods strongly conduplicate,
         with a conspicuous radially compressed crest....8. ASCLEPIODOLUS
   BB. Hoods thickly involute-clavate.
      C. Corolla lobes reflexed; hoods with deeply bifid alternating lobules;
         translator arms very long........................9. ANANTHERIX

CC. Corolla lobes ascending; hoods with entire alternating lobules; trans-
          lator arms of moderate length..................10. ASCLEPIODORA
AA. Corolla rotate-subtubular, the lobes erect or only slightly spreading;
     anther head borne on a slender stipe high above the corona.........
     ....11. PODOSTIGMA

This key will not be of great use to those who are not thoroughly familiar with the varying structure of the Milk-weed flower. The monograph of the genus which I am preparing will contain the discussion and illustrations of the criteria necessary for general use.

To many readers familiar with the segregate genera of *Asclepias* in a restricted region of the United States, the reduction of such well-established entities as *Acerates, Asclepiodora,* and *Podostigma* may appear as an admission of casual superficiality. Let them study the scores of species of *Asclepias* represented in North America, intensively, for several years, however (and above all, let them attempt to compose an adequate key even to subgenera and sections), and I am convinced that those without prejudice will appreciate the practical and theoretical advantages of ''lumping.'' Fortunately, very few new combinations are necessary by interpreting the genus in a broad sense, for practically all species have been described under *Asclepias* at one time or another. The relatively few exceptions amongst the species with which I am familiar at present are treated under their respective subgenera as follows:

SUBGENUS 1. EUASCLEPIAS

ASCLEPIAS **hypoleuca** (A.Gray) Woodson, comb. nov.
   Gomphocarpus hypoleucus A.Gray, Proc. Amer. Acad. **17**: 222. 1881–82.
ASCLEPIAS **Phenax** Woodson, nom. nov.
   Acerates humilis Benth. Pl. Hartw. 291. 1848, non *Asclepias humilis* Schltr.
ASCLEPIAS **Pringlei** (Greenm.) Woodson, comb. nov.
   Acerates Pringlei Greenm. Proc. Amer. Acad. **34**: 570. 1899.

SUBGENUS 5. ACERATES

ASCLEPIAS **hirtella** (Pennell) Woodson, comb. nov.

Acerates hirtella Pennell, Bull. Torrey Club **46**: 184. 1919.

SUBGENUS 6. POLYOTUS

ASCLEPIAS **Engelmanniana** Woodson, nom. nov.

Acerates auriculata Engelm. in Torr. Rept. Bot. Mex. Bound. Surv. 160. 1859.

Asclepias auriculata (Engelm.) Holzinger, Bot. Gaz. **17**: 125, 160. 1892, non HBK.

SUBGENUS 7. SOLANOA

ASCLEPIAS **Solanoana** Woodson, nom. nov.

Gomphocarpus purpurascens A.Gray, Proc. Amer. Acad. **10**: 76. 1874, non A.Rich.

Schizonotus purpurascens A.Gray, loc. cit. **12**: 66. 1877.

Solanoa purpurascens (A.Gray) Greene, Pittonia **2**: 67. 1890.

Solanoana purpurascens (A.Gray) O.Ktze. Rev. Gen. **2**: 421. 1891.

SUBGENUS 8. ASCLEPIODOLUS

ASCLEPIAS **insignis** (Brandg.) Woodson, comb. nov.

Asclepiodora insignis Brandg. Zoe **5**: 253. 1908.

SUBGENUS 10. ASCLEPIODORA

ASCLEPIAS **circinalis** (Dcne.) Woodson, comb. nov.

Acerates circinalis Dcne. Ann. Sci. Nat. Bot. ii. **9**: 322. *pl. 10, fig. c.* 1838.

Asclepiodora circinalis (Dcne.) Fourn. loc. cit. vi. **14**: 369. 1882.

ASCLEPIAS **Fournieri** Woodson, nom. nov.

Acerates gomphocarpoides Dcne. Ann. Sci. Nat. Bot. ii **9**: 323. 1838, non *Asclepias gomphocarpoides* Schltr.

Asclepiodora gomphocarpoides (Dcne.) Fourn. loc. cit. vi. **14**: 369. 1882.

ASCLEPIAS **zanthodacryon** (Smith & Harris) Woodson, comb. nov.

Asclepiodora zanthodacryon Smith & Harris, Contr. Gray Herb. **114**: 12. 1936.

II. Oxypetalum R.Br. Mem. Wern. Soc. 1: 41. 1809.

Apparently *O. cordifolia* (Vent.) Schltr. is the only representative of this troublesome genus in Central America and the Antilles. Fortunately, this species has strongly appendaged translator arms which enable it to be separated easily from *Cynanchum*. But in South America there are many species without this diagnostic structure, the importance of which will present one of the major problems of the Asclepiads in the southern continent.

III. Cynanchum L. Sp. Pl. 212. 1753.

Ditassa R.Br. Mem. Wern. Soc. 1: 49. 1809.
Metastelma R.Br. loc. cit. 52. 1809.
Enslenia Nutt. Gen. N. Am. Pl. 1: 164. 1818, non Raf.
Ampelamus Raf. Amer. Monthly Mag. 4: 192. 1819.
Lyonia Ell. Sketch Bot. S. Carol. 1: 316. 1821, non Nutt.
Seutera Reichenb. Consp. 131. 1828.
Enslinia Reichenb. loc. cit. 1828.
Roulinia Dcne. in DC. Prodr. 8: 516. 1844, non A. Brongn.
Orthosia Dcne. loc. cit. 526. 1844.
Tassadia Dcne. loc. cit. 579. 1844.
Irmischia Schlecht. Linnaea 19: 738. 1847.
Nanaturis Turcz. Bull. Soc. Nat. Mosc. 21^1: 254. 1848.
Amphistelma Griseb. Fl. B.W.I. 417. 1861.
Tylodontia Griseb. Cat. Pl. Cub. 175. 1866.
Metalepis Griseb. loc. cit. 179. 1866.
Mellichampia A.Gray, Proc. Amer. Acad. 22: 437. 1887.
Pattalias S.Wats. loc. cit. 24: 60. 1889.
Tainionema Schltr. in Urb. Symb. Ant. 1: 263. 1899.
Decastelma Schltr. loc. cit. 264. 1899.
Rouliniella Vail, Bull. Torrey Club 29: 662. 1902.
Basistelma Bartlett, Proc. Amer. Acad. 44: 631. 1909.
Epicion Small, Man. Fl. 1075. 1933.
Astephanus of American authors.

Besides the preceding, several synonyms eventually will have to be added from the South American flora. Very few of

these synonymous genera are absolutely co-extensive, since
they are based for the greater part upon variations of the
corona. Because these differences are multitudinous but of the
same general *motif,* the practical solution of the problem ap-
pears to lie in an inclusive treatment, such as that adopted for
Asclepias. The principal characters used to separate the seg-
regates just enumerated are aestivation of the corolla lobes
(whether contorted or valvate—extremely difficult to observe
in most species), corona (whether simple or compound, deeply
or less deeply divided, or absent), and structure of the inflo-
rescence (whether racemiform or umbelliform—since the basic
structure is cymose for all, this distinction resolves itself into
a comparison of internode length). These characters combine
kaleidoscopically in so many manners, and frequently result in
the separation into different genera of so many species of ob-
vious affinity, that they appear of very doubtful value. I am
inclined to discount particularly the value of corolla aestiva-
tion and corona structure, and to group the North American
species under the following subgenera. These I am illustrating
with representative adjustments in nomenclature.

KEY TO THE SUBGENERA

A. Cymes racemiform to corymbiform, with definitely manifest internodes.
  B. Corolla campanulate to rotate-subcampanulate, the throat not con-
     stricted at the orifice.
    C. Corona lobes relatively elongate, free or united only at the bases.
      D. Corona lobes acuminate, entire or with very obscure lateral lobules
        ....1. MELLICHAMPIA
      DD. Corona lobes deeply bifid.......................2. AMPELAMUS
    CC. Corona cyathiform, broadly and shallowly lobed, the lobes broadly
      emarginate ....3. METALEPIS
  BB. Corolla urceolate, the throat constricted at the orifice....4. TYLODONTIA
AA. Cymes umbelliform, usually without the appearance of definite internodes.
  B. Corolla lobes ascending or spreading.................5. METASTELMA
  BB. Corolla lobes inflexed-cucullate.....................6. CLEISTOLOBUS

SUBGENUS 1. MELLICHAMPIA

CYNANCHUM **jaliscanum** (Vail) Woodson, comb. nov.
    Rouliniella jaliscana Vail, Bull. Torrey Club **29:** 668.
      1902.

Cynanchum **jamaicense** (Griseb.) Woodson, comb. nov.

Enslenia jamaicensis Griseb. Fl. B.W.I. 418. 1861.

Rouliniella jamaicensis (Griseb.) Rendle, Journ. Bot. **74:** 340. 1936.

Cynanchum **lignosum** (Vail) Woodson, comb. nov.

Rouliniella lignosa Vail, Bull. Torrey Club **29:** 666. 1902.

Cynanchum **ligulatum** (Benth.) Woodson, comb. nov.

Enslenia ligulata Benth. Pl. Hartw. 290. 1848.

Mellichampia rubescens A.Gray, Proc. Amer. Acad. **22:** 437. 1887.

Ampelamus ligulatus (Benth.) Heller, Contr. Herb. Franklin & Marshall Coll. **1:** 79. 1895.

Mellichampia ligulata (Benth.) Vail, Bull. Torrey Club **26:** 425. 1899.

Roulinia ligulata (Benth.) Pittier, Contr. U.S. Nat. Herb. **13:** 111. 1910, as to synonymy.

Cynanchum **Rensoni** (Pittier) Woodson, comb. nov.

Roulinia Rensoni Pittier, Contr. U.S. Nat. Herb. **13:** 101. 1910.

Cynanchum **saepimentorum** (Brandg.) Woodson, comb. nov.

Vincetoxicum saepimentorum Brandg. Univ. Cal. Publ. Bot. **4:** 381. 1913.

Cynanchum **sinaloense** (Brandg.) Woodson, comb. nov.

Roulinia sinaloensis Brandg. Zoe **5:** 243. 1908.

Mellichampia sinaloensis (Brandg.) Kearney & Peebles, Journ. Wash. Acad. Sci. **29:** 488. 1939.

Cynanchum **unifarium** (Scheele) Woodson, comb. nov.

Gonolobus unifarius Scheele, Linnaea **21:** 760. 1848.

Roulinia unifaria (Scheele) Engelm. in Torr. Rept. Bot. Mex. Bound. Surv. 160. 1859.

Rouliniella unifaria (Scheele) Vail, Bull. Torrey Club **29:** 663. 1902.

Cynanchum **Watsonianum** Woodson, nom. nov.

Roulinia Palmeri S.Wats. Proc. Amer. Acad. **18:** 115. 1883, non *Cynanchum Palmeri* (Wats.) Blake *(Pattalias Palmeri* Wats.).

Rouliniella Palmeri (S.Wats.) Vail, Bull. Torrey Club **29:** 664. 1902.

Ampelamus, Rouliniella, and *Mellichampia* can be recognized as genera only by extremely tenuous criteria. As far as I am aware, the first would have to be supported by the bifid corona segments and the rostrate stigma head; the second by a flat (or scarcely conical) stigma head and acuminate crown segments, although they are slightly emarginate in some species and not infrequently show a tendency toward the development of marginal lobules; the third would have to depend upon *somewhat* larger flowers than *Rouliniella, somewhat* more nearly campanulate corollas, and crown segments *somewhat* more united at the base. *Mellichampia* also has a stigma head intermediate between that of *Ampelamus* and that of *Rouliniella.* The crown segments of *Ampelamus* and of *Mellichampia* are flat; those of *Rouliniella* are usually *somewhat* cucullate or infolded at the base.

The primary division of the key to subgenera advocated here is one that will have to be used in some cases with a certain degree of experience, if not prejudice. Whilst the inflorescence of the *Mellichampia*-complex may be described as racemiform generally, and that of the *Metastelma*-complex as umbelliform, ambiguous species occur in both groups quite frequently enough to support my contention that it is impractical to maintain a series of distinct genera. Whilst the flowers of the *Mellichampia*-complex are smaller, as a rule, than those of the *Metastelma*-complex, this is in the nature of a guiding ''prejudice'' only. I have been unable to discover supporting structural characters of merit.

SUBGENUS 2. AMPELAMUS

CYNANCHUM LAEVE (Michx.) Pers. Syn. **1**: 274. 1805.

Gonolobus laevis Michx. Fl. Bor. Am. **1**: 119. 1803.

Enslenia albida Nutt. Gen. N.Am. Pl. **1**: 165. 1818.

Ampelanus albidus (Nutt.) Britton, Bull. Torrey Club **21**: 314. 1894.

The interpretation of this species has been singularly confused. In 1803 Michaux (loc. cit.) founded *Gonolobus* with three species, two of which previously had constituted the whole complement of the earlier genus *Vincetoxicum* Walt.

(Fl. Carol. 104. 1788): *G. macrophyllus (V. gonocarpos* Walt.), and *G. hirsutus (V. acanthocarpus* Walt.). The third species, *G. laevis,* originated with Michaux.

It is important in this connection to emphasize certain morphological characters of the fruit as embodied in the generic and specific descriptions by Michaux. For the genus as a whole: *"Folliculi plerumque costati seu angulosi. . ."* The follicles of the three species were described as follows: *G. macrophyllus—"folliculis costato-angulosis"*; for *G. hirsutus—"folliculis oblongis, sparsim muricatis"*; but for *G. laevis—"folliculis laevibus."* It is obvious that the smooth condition of the fruit of *G. laevis*—not angled as in *macrophyllus,* nor muricate as in *hirsutus*—was particularly outstanding in the estimation of Michaux, and that it suggested the specific adjective itself.

The type specimens of *G. laevis,* if they may be called such, have been examined both by Dr. Gray (Proc. Amer. Acad. Sci. **12**: 75. 1877) and by Miss Vail (Bull. Torrey Club **26**: 427. 1899), and both agreed that at least two elements are represented amongst the fragments, namely, flowers and angled fruits of *G. suberosus* (L.) R.Br.—of which *G. macrophyllus* Michx. *(G. gonocarpos* (Walt.) Perry) probably is no more than a variety—and leaves of the slender vine currently known as *Enslenia albida* Nutt. or *Ampelanus* (correctly *Ampelamus) albidus* (Nutt.) Britton. But Dr. Gray chose the flowers and fruit as authentic, whilst Miss Vail chose the leaves. At first glance Miss Vail's selection may appear to be with little foundation, until it is recalled that Michaux stipulated for his species *"folliculis laevibus,"* exactly the condition of *Ampelamus;* and that in choosing the material with angled pods, Dr. Gray denied the diagnostic character of the species. In such an instance, of obviously accidental mixture, the evident solution is to accept, as typical, material known to coincide with the original literature.

Had she studied her problem under existing rules of nomenclature, Miss Vail certainly would have placed *laevis* in a new combination under *Ampelamus.* Under the interpretations current at the New York Botanical Garden during that

time, however, she invoked the "Doctrine of Residues," re-
turning *G. macrophyllus* and *G. hirsutus* to *Vincetoxicum*
Walt., from which they had been taken by Michaux, and re-
taining the name *Gonolobus* for *G. laevis*.

In this connection, however, it should be noted that Michaux
embodied in his diagnosis of *Gonolobus* two characters which
do not coincide with the present interpretation of *G. laevis*:
"*Stylus discoideo-5-gonus. . . Folliculi plerumque costati seu
angulosi.*" The absence of a "Doctrine of Residues" notwith-
standing, therefore, I feel that Miss Perry (Rhodora **40**: 283.
1938) is quite correct in considering the Walterian element
as typical of *Gonolobus*, choosing *G. macrophyllus* as the
standard species. Nevertheless, one feels that sentiment may
have induced her to perpetuate Dr. Gray's interpretation of
G. laevis rather than the more logical conclusion of Miss Vail.

Although it does not bear directly upon the question of
G. laevis, it might be well to explain here, for future refer-
ence, that although *Vincetoxicum* Walt. clearly antedates
Gonolobus Michx., as well as *Vincetoxicum* Moench (Meth.
717. 1794), the nomenclatorial powers at Kew, invoked by
Miss Perry (loc. cit. 281–282. 1938), "temporarily" have
placed *Vincetoxicum* Moench on the list of *Nomina Con-
servanda,* tantamount to final acceptance, since "the European
Vincetoxicum is so widely used that there is every chance of
its being conserved" (passage of letter by Mrs. T. A. Sprague,
as quoted by Miss Perry). I suspect that the European Ascle-
piadologists, having had *Vincetoxicum* Moench conserved for
them, will scarcely know how to use it: its distinction from
Cynanchum is extremely evasive.

SUBGENUS 3. METALEPIS

CYNANCHUM **cubense** (Griseb.) Woodson, comb. nov.

Metalepis cubensis Griseb. Cat. Pl. Cub. 179. 1866.

The inclusion of *Metalepis* within the Gonolobeae by Schu-
mann (in Engl. & Prantl, Nat. Pflanzenfam. **4²**: 297. 1895) is
a conspicuous instance of the ambiguity of the current defini-
tions of the tribes of Asclepiadaceae. The pollinia in the
species of this subgenus are quite pendulous, with the equally

rounded surfaces characteristic of the Asclepiadeae, but the translators are very long and horizontal, a condition found exactly duplicated in a few species of the subgenus *Mellichampia*. Aside from this character, the subgenus depends upon the racemiform inflorescences and the cyathiform corona, the inadequacy of which, as generic characters, has been noted previously.

SUBGENUS 4. TYLODONTIA

CYNANCHUM **Grisebachii** (Maza) Woodson, comb. nov.

Tylodontia cubensis Griseb. Cat. Pl. Cub. 179. 1866, non *Cynanchum cubense* (Griseb.) Woodson *(Metalepis cubensis* Griseb.).

Astephanus Grisebachii Maza, Cat. Periant. 276. 1894.

Tylodontia has been included as a synonym under *Astephanus* by Schumann (in Engl. & Prantl, Nat. Pflanzenfam. 4²: 224. 1895), but dissection of flowers from an isotype *(Wright 2964)* in the herbarium of the Missouri Botanical Garden shows the presence of a corona of five erose, truncated scales. The subgenus is outstanding in the *Mellichampia*-complex because of the small flowers having urceolate corollas with sharply reflexed lobes.

SUBGENUS 5. METASTELMA

At present I do not feel sufficiently familiar with the synonymy of *Metastelma* to attempt the many nomenclatural changes necessary for inclusion in *Cynanchum*. This is the most difficult of the American groups of Asclepiads because the flowers are so small. Within the tiny corollas, averaging only about 2 mm. in length, are packed as many structural details and variations as within the larger flowers of other genera. Once when I was complaining to Dr. Standley of the eye and nerve strain necessary in dealing with the group, he laughingly agreed that it should be studied by an algologist or a mycologist.

Metastelma will be handled very much easier, I believe, if it is treated as a single subgenus under *Cynanchum*. Unquestionably the various entities included here are much more closely related to one another than to any other complex. The

whole aspect of the plants is so unmistakable that I feel, even with convenience particularly in mind, that "lumping" is natural as well.

As has been remarked in a previous paragraph, *Astephanus* is difficult to maintain upon a sure foundation even with the higher powers of a binocular dissecting microscope. Amongst several specimens ascribed to *A. pubescens* Greenm. in the herbarium of the Missouri Botanical Garden are two entities, one with a manifest corona and one without, the anthers of the two species differing considerably; yet the superficial aspects of the plants are all but undistinguishable. Natural genera should not be so easily confused.

Many readers may be surprised at the inclusion of *Ditassa* and *Decastelma* with *Metastelma*. But the cleaving of the corona scales or the presence of a ventral tooth or ligule, which distinguish these entities from *Metastelma* (sensu stricto), are found amongst the Old World Cynancha as well as in the *Mellichampia*-complex of Central America. Similar variation also is found in *Asclepias*.

SUBGENUS 6. CLEISTOLOBUS

CYNANCHUM **utahense** (Engelm.) Woodson, comb. nov.

Astephanus utahensis Engelm. Amer. Nat. **9**: 349. 1875.

The inflexed-cucullate corolla lobes of this species, unlike those of any other known to me, were interpreted by Dr. Engelmann as a modification to compensate for the absence of a corona.

IV. BLEPHARODON Dcne. in DC. Prodr. **8**: 603. 1844.

The nine species assigned to *Blepharodon* by Decaisne fall into two groups superficially marked by volubile or erect herbaceous habits, but accompanied by interesting differences in the corona and pollinia as well. Although I may seem inconsistent in view of my treatment of generic lines generally in this family, I feel that two distinct genera may be represented. The North American species are all of the volubile group (with the exception of *B. neriifolium* Dcne., which I believe

probably will be found to be an *Asclepias* when the material
is available for study), and since this group seems to have
been more typical of the genus in the opinion of Decaisne, I
am reserving the use of the generic name for that connection.
In respect for the memories of the many genera that I have
reduced to synonymy during these studies, I am deferring
judgment on the generic status of the erect species until I have
the opportunity to devote my attention to the South American
Asclepiads.

V. Sarcostemma R.Br. Mem. Wern. Soc. **1**: 50. 1809.

Philibertia HBK. Nov. Gen. **3**: 195. 1819.
Pentagonium Schauer, Nova Acta Acad. Caes. Leop. Nat. Cur.
    19. Suppl. 1: 364. 1843.
Zosima Phil. Sert. Mendoz. Alt. 29. 1871.
Funastrum Fourn. Ann. Sci. Nat. Bot. vi. **14**: 388. 1882.
Cystostemma Fourn. in Mart. Fl. Bras. **6**[4]: 204. 1885.
Philibertella Vail, Bull. Torrey Club **24**: 305. 1897.
Ceramanthus Malme, Ark. Bot. **4**[14]: 2. 1905.

A few additional synonyms will have to be added from the
South American flora. I am very reluctant to disregard
Schlechter's separation of *Philibertia* and *Funastrum* (in
Fedde, Repert. **13**: 279–287. 1915), but feel that it is necessary
to do so in order to maintain balance within the family. As far
as I am aware, the only character really separating the two
entities, upon the basis of present speciation, is the structure
of the corolla, whether campanulate with shallow lobes in the
former, or rotate with more deeply divided lobes in the latter.
Other definitive structures apparently are lacking, and the
striking similarity, if not identity, of the anther, pollinia, and
corona characters is impressive. The high attachment of the
corona bladders to the anthers, cited by Schlechter for *Phili-
bertia,* manifestly does not hold. The annulus connecting the
bladdery corona segments is usually more pronounced in
Funastrum than in *Philibertia,* but is present in both. *Sarco-
stemma,* currently interpreted as including only Old World
species, was erected by Robert Brown to include species now

relegated to *Funastrum* and *Philibertia* as well. I can find no
tangible distinction between the three, although they were
placed in different subtribes by Schumann, as has been ex-
plained previously. Few North American species have been
described since the prevalence of the restricted definition of
Sarcostemma, and only the following transfers appear to be
necessary:

SARCOSTEMMA **tomentella** (Brandg.) Woodson, comb. nov.
  Philibertia tomentella Brandg. Univ. Cal. Publ. Bot. **4**: 90.
    1910.

SARCOSTEMMA **Torreyi** (A.Gray) Woodson, comb. nov.
  Philibertia Torreyi A.Gray, Proc. Amer. Acad. **12**: 64.
    1877.
  Philibertella Torreyi (A.Gray) Vail, Bull. Torrey Club
    24: 309. 1897.
  Funastrum Torreyi (A.Gray) Schltr. in Fedde, Repert.
    13: 287. 1915.

VI. MATELEA Aubl. Fl. Guian. **1**: 277. *t.109.* 1775.

Hostea Willd. Sp. Pl. **1**: 1274. 1798.
Macroscepis HBK. Nov. Gen. **3**: 200. 1819.
Pherotrichis Dcne. Ann. Sci. Nat. Bot. ii. **9**: 322. 1838.
Ibatia Dcne. in DC. Prodr. **8**: 599. 1844.
Polystemma Dcne. loc. cit. 602. 1844.
Dictyanthus Dcne. loc. cit. 604. 1844.
Chthamalia Dcne. loc. cit. 605. 1844.
Ptycanthera Dcne. loc. cit. 606. 1844.
Trichosacme Zucc. Abh. Akad. Wiss. München **4²**: 11. 1845.
Tympananthe Hassk. Flora **30**: 757. 1847.
Rytidoloma Turcz. Bull. Soc. Nat. Mosc. **25²**: 319. 1852.
Callaeolepium Karst. Fl. Col. **2**: 123. 1865.
Poicilla Griseb. Cat. Pl. Cub. 176. 1866.
Himantostemma A.Gray, Proc. Amer. Acad. **20**: 294. 1885.
Rothrockia A.Gray, loc. cit. 295. 1885.
Tetracustelma Baill. Hist. Pl. **10**: 292. 1891.
Urostephanus Robins. & Greenm. Amer. Journ. Sci. iii. **50**:
  159. 1895.

Prosthecidiscus Donn.Sm. Bot. Gaz. **25**: 149. 1898.
Labidostelma Schltr. Bull. Herb. Boiss. ii. **6**: 843. 1906.
Microdactylon Brandg. Zoe **5**: 252. 1908.
Amphorella Brandg. Univ. Cal. Publ. Bot. **4**: 91. 1910.
Poicillopsis Schltr. in Urb. Symb. Ant. **7**: 339. 1912.
Pachystelma Brandg. Univ. Cal. Publ. Bot. **7**: 330. 1920.
Cyclodon Small, Man. Fl. 1075. 1933.
Odontostephana Alexander, in Small, loc. cit. 1076. 1933.
Edisonia Small, loc. cit. 1078. 1933.
Heliostemma Woodson, Amer. Journ. Bot. **22**: 689. 1935.
Gonolobus and *Vincetoxicum* of North American authors, in
    large part.

To this imposing list of synonyms eventually will have to be
added numerous generic names from the South American flora.
Very few of these entities are strictly co-extensive, nearly all
having been based upon some more or less striking variation
of the corona. Loud protestations probably will be made by
botanists familiar with such extremes as *Dictyanthus* and
Macroscepis that at least those familiar genera should be
allowed to stand inviolate, but I should like to lay a curse on
the man who revives them without at least as much study as I
have devoted. And I feel compelled to enjoin all future sys-
tematists to ponder long and deeply the intricacies of the
gonoloboid corona before proposing additional novelties.

The corona of *Matelea*, as is almost universal in the Cynan-
choideae, consists of a unit enation of the anther filament,
fundamentally subtending an additional enation (such as the
hood and horn, respectively, of most species of *Asclepias*).
The outer units may be separate, essentially entire, or with
variously elaborated marginal lobules; at other times they
may be concrescent into an inconspicuous, fimbriate skirt at
the base of the gynostegium, into a ring, or into a massive ro-
tate disc adnate to the corolla throat. The inner units may be
small appendages of the anther head stipe rather high above
the outer units, or may be combined, either essentially free
or completely adnate, with the outer units. The result is a
kaleidoscopic medley that can be conveyed in print only by the
use of critical illustrations for each of the dozens of species.

At one time during the studies which preceded this paper, an intensive study was made of the anther structure of the Gonoloboids, for I felt that the position of the anthers with respect to the stigma head (whether beneath or about the margin) would aid in the establishment of some of the favorite genera apparently doomed to synonymy. Here numerous trends were obvious, but nothing of sufficient stability for generic distinction. A long consideration of pollinium structure also was ended in rather bitter frustration.

A peculiar vegetative character which links practically all the species groups of *Matelea* (although by no means every species of the groups) is the mixed indument consisting of long eglandular hairs and short, bulbose emergences. These emergences usually appear to be somewhat glandular, and may be white, dark brown, or black. Since no other group of Asclepiads with which I am familiar possesses such an indument, with the exception of the closely neighboring *Fischeria* maintained provisionally and with some misgivings, I regard its occurrence in *Matelea* as extremely significant. I am convinced that the elements which I have included in that genus are inextricably related.

Heretofore, *Matelea* has been a genus of perhaps four South American species poorly represented in North American herbaria. Its expansion as advocated here consequently entails a shocking number of new combinations. Only a few of the generic synonyms (such as *Macroscepis* and *Dictyanthus*) contain as many as half a dozen species, however, and in view of that fact and the many nomenclatural changes necessary in any event it seems scarcely worth while to ask conservation for any of those names. Then, too, such a drastic reformation may better be served by a poorly known generic name than by one with more definitely established associations.

Recent tropical American collections are bringing to light more novelties in *Matelea* than perhaps in any other genus of Asclepiads. Therefore I have prepared the following key to subgenera and sections, both to illustrate the reformation of the genus and as a temporary aid to herbarium study. I have treated several groups as subgenera simply because they have

familiar names and in spite of the fact that their characters are less important than certain others which are treated as sections, having no previous generic name (for I am wary of treating them as nouns lest some floristic student raise them to genera). As accumulation of Asclepiads from tropical North America proceeds, additional entries will have to be inserted in the key. That should accentuate the greater convenience of an ultra-conservative generic concept. As a final word, it should be emphasized that the species groups show great variation amongst their constituents, and that they cannot safely be raised to generic rank as they now exist. Certain species show affinities for more than one group. Where I have made an arbitrary disposition in such cases I usually have included notes or references to aid their identification.

Key to the Subgenera and Sections

A. Pollinia more or less descending from the translator arms.
  B. Corolla subcampanulate-rotate, without a faucal annulus, the limb merely continuing the dilation of the throat and much longer than it; corona annular, the 5 constituent segments usually distinctly 3-lobed; pollinia frequently prolonged beyond the attachment of the translator arms, excavated on one face only............1. IBATIA
  BB. Corolla very broadly campanulate, the lobes very broad and scarcely as long as the shallow open throat, without a faucal annulus; corona rotate, of 5 segments consisting of 2 falcate outer lobes and a median inflexed lobule; pollinia conspicuously excavated on both faces..2. LABIDOSTELMA
  BBB. Corolla salverform-rotate, usually with a faucal annulus, the limb abruptly spreading or somewhat reflexed from the short tube.
    C. Corolla lobes without caudate appendages; corona of 5 digitate segments adnate to the corolla tube, each with a more or less distinct callous boss supporting the stigma head; pollinia without apical processes; plants variously pubescent, but not white-woolly......
    ....3. MACROSCEPIS
    CC. Corolla lobes with long plumose caudate appendages; corona annular, shallowly 5-lobed, each lobe with an inconspicuous internal ligule; pollinia with a slender apical process; entire plant very densely white-woolly..........................4. TRICHOSACME
AA. Pollinia essentially horizontal, but occasionally arcuate, with the tips somewhat ascending or descending.
  B. Antillean species (corolla rotate; if deeply campanulate, see *Pachystelma*).

C. Corona of 5 broad barely united segments each bearing a conspicu-
   ous incurved hook or ligule; anther head very shortly stipitate
   ....5. POICILLA
CC. Corona not as above............................6. PTYCANTHERA
   D. Anther head distinctly stipitate.......................§. *Pauciflorae*
   DD. Anther head absolutely sessile........................§. *Variifoliae*
BB. Continental species.
   C. Pollinia subquadrate- or oblong-reniform with a narrow hyaline
      margin; corona of 5 more or less united segments each with an
      internal ligule or boss.........................7. CHTHAMALIA
   CC. Pollinia falciform or arcuate, the tips markedly ascending, hyaline
      margins or indentations inconspicuous or lacking.
      D. Erect or prostrate herbs; corolla lobes ascending.
         E. Corolla rotate-subcampanulate, the orifice not constricted;
            corona segments not strongly adnate to the corolla throat
            ....8. PHEROTRICHIS
         EE. Corolla urceolate-campanulate, the orifice markedly constricted;
            corona strongly adnate to the corolla throat...9. AMPHORELLA
      DD. Lianas or twining undershrubs (except *M. caudata*); corolla lobes
         reflexed or spreading.
         E. Corolla rotate, with long narrow ascending lobes; corona of
            5 nearly separate pectinate segments; anther head with a
            definite appendiculate stipe..............10. TIARASTEMMA
         EE. Corolla deeply campanulate, with relatively broad ascending
            lobes; corona of 5 fimbriately compound segments; anther
            head sessile...........................11. POLYSTEMMA
         EEE. Corolla subcampanulate-rotate, with relatively broad widely
            spreading or reflexed lobes; corona of 5 broad, more or less
            carunculate segments usually strongly adnate to the corolla
            throat; anther head sessile...............12. HELIOSTEMMA
   CCC. Pollinia subtriangular-pyriform, with a conspicuous hyaline indenta-
      tion or margin and broad winged translator arms.
      D. Corolla rotate to subcampanulate-rotate; anther head round to very
         broadly 5-gonal; corona more or less annular or rotate.........
         ....13. EUMATELEA
         E. Corolla without a faucal annulus exterior to the true corona.
            F. Anther head with a strongly manifest fluted stipe..§. *Reticulatae*
            FF. Anther head essentially sessile; corona with 5 broad parti-
               tions superposed.
               G. Corona light and intricately fimbriate..........§. *Violaceae*
               GG. Corona dark and carunculate.............§. *Pseudobarbatae*
         EE. Corolla throat with an interrupted 5-angled faucal annulus ex-
            terior to the true corona.......................§. *Viridiflorae*
      DD. Corolla deeply campanulate; anther head saliently 5-gonal; corona
         of 5 simple or compound digitate segments.
         E. Corona segments digitately compound, adnate to the column
            but essentially free from the corolla; corolla lobes strikingly
            pilose-barbate within.................14. MICRODACTYLON

EE. Corona segments simply digitate or merely somewhat caruncu-
       late, adnate to the corolla throat at least at the base; corolla
       lobes essentially glabrous within.
   F. Corona lobes relatively short and thick, adnate to the corolla
         only at the base; corolla lobes flat......15. PACHYSTELMA
   FF. Corona lobes long and narrow, wholly adnate to the corolla
         throat and imbedded in similarly shaped fleshy corolline
         excrescences; corolla lobes sharply revolute, especially at
         the base.............................16. DICTYANTHUS

SUBGENUS 1. IBATIA

MATELEA **araneosus** (Donn.Sm.) Woodson, comb. nov.
   Gonolobus araneosus Donn.Sm. Bot. Gaz. **47**: 257. 1909.
MATELEA **atrocoronata** (Brandg.) Woodson, comb. nov.
   Vincetoxicum atrocoronatum Brandg. Univ. Cal. Publ.
      Bot. **6**: 372. 1917.
MATELEA **chrysantha** (Greenm.) Woodson, comb. nov.
   Gonolobus chrysanthus Greenm. Proc. Amer. Acad. **32**:
      299. 1897.
   Vincetoxicum chrysanthum (Greenm.) Standl. Contr.
      U.S. Nat. Herb. **23**: 1190. 1924.
MATELEA **cordifolia** (A.Gray) Woodson, comb. nov.
   Rothrockia cordifolia A.Gray, Proc. Amer. Acad. **20**: 295.
      1885.
MATELEA **fruticosa** (Brandg.) Woodson, comb. nov.
   Rothrockia fruticosa Brandg. Zoe **5**: 165. 1903.
MATELEA **gonoloboides** (Robins. & Greenm.) Woodson, comb.
   nov.
   Urostephanus gonoloboides Robins. & Greenm. Amer.
      Journ. Sci. iii. **50**: 159. 1895.
MATELEA **inconspicua** (Brandg.) Woodson, comb. nov.
   Gonolobus inconspicuus Brandg. Univ. Cal. Publ. Bot. **3**:
      387. 1909.
MATELEA **maritima** (Jacq.) Woodson, comb. nov.
   Cynanchum maritimum Jacq. Stirp. Amer. 83. *pl.56*.
      1763.
   Gonolobus maritimus (Jacq.) R.Br. Mem. Wern. Soc. **1**:
      35. 1809.
   Gonolobus floccosus Bertol. Opusc. **4**: 521. 1823.
   Gonolobus suberosus Spreng. Syst. **1**: 846. 1825, non
      R.Br.

Ibatia maritima (Jacq.) Dcne. in DC. Prodr. **8**: 599. 1844.

Lachnostoma maritimum (Jacq.) Nichols. Dict. Gard. **2**: 236. 1884.

Ibatia muricata Griseb. Fl. B.W.I. 421. 1861.

Matelea **mollis** (Griseb.) Woodson, comb. nov.

Ibatia mollis Griseb. Cat. Pl. Cub. 177. 1866.

Lachnostoma molle (Griseb.) Maza, Cat. Periant. 276. 1894.

Ptychanthera mollis (Griseb.) Schltr. in Urb. Symb. Ant. **1**: 280. 1899.

Matelea **patalensis** (Donn.Sm.) Woodson, comb. nov.

Gonolobus patalensis Donn.Sm. Bot. Gaz. **47**: 256. 1909.

Matelea **petiolaris** (A.Gray) Woodson, comb. nov.

Gonolobus petiolaris A.Gray, Proc. Amer. Acad. **21**: 397. 1886.

Vincetoxicum petiolare (A.Gray) Standl. Contr. U.S. Nat. Herb. **23**: 1189. 1924.

Matelea **porphyrantha** (Standl.) Woodson, comb. nov.

Vincetoxicum porphyranthum Standl. ex Yuncker, Field Mus. Publ. Bot. **17**: 387. 1938.

Matelea **Pringlei** (A.Gray) Woodson, comb. nov.

Himantostemma Pringlei A.Gray, Proc. Amer. Acad. **20**: 294. 1885.

Matelea **Prosthecidiscus** Woodson, nom. nov.

Prosthecidiscus guatemalensis Donn.Sm. Bot. Gaz. **25**: 150. *pl.12.* 1898, non *Matelea guatemalensis* (K.Sch.) Woodson.

Matelea **pueblensis** (Brandg.) Woodson, comb. nov.

Vincetoxicum pueblensis Brandg. Univ. Cal. Publ. Bot. **4**: 91. 1910.

Matelea **Purpusii** (Brandg.) Woodson, comb. nov.

Gonolobus Purpusii Brandg. Univ. Calif. Publ. Bot. **3**: 387. 1909.

Matelea **tristiflora** (Standl.) Woodson, comb. nov.

Vincetoxicum tristiflorum Standl. Field Mus. Publ. Bot. **17**: 272. 1937.

Matelea **umbellata** (Brandg.) Woodson, comb. nov.

Rothrockia umbellata Brandg. Zoe **5**: 165. 1903.

MATELEA **Warscewiczii** (Karst.) Woodson, comb. nov.

Callaeolepium Warscewiczii Karst. Fl. Col. **2**: 123. *pl. 165*. 1865.

Fimbristemma Warscewiczii (Karst.) Benth. & Hook. Gen. Pl. **2**: 768. 1876.

Ibatia is placed in the key as having "pendulous" pollinia since their vertical dimension is at least equal to the horizontal and usually is greater. Some confusion with *Chthamalia* is likely to occur, but may be avoided by a comparison of the coronas, that of the former subgenus being without internal ligules or bosses adnate to the segments and that of the latter always having such structures.

SUBGENUS 2. LABIDOSTELMA

MATELEA **Quirosii** (Standl.) Woodson, comb. nov.

Cynanchum rotatum Sesse & Mociño, Fl. Mex. 76. 1887, non Vell.

Labidostelma guatemalense Schltr. Bull. Herb. Boiss. ii. **6**: 843. 1906, non *M. guatemalensis* (Donn.Sm.) Woodson.

Vincetoxicum Quirosii Standl. Field Mus. Publ. Bot. **18**³: 959. 1938.

SUBGENUS 3. MACROSCEPIS

MATELEA **calcicola** (Greenm.) Woodson, comb. nov.

Gonolobus calcicola Greenm. Proc. Amer. Acad. **40**: 30. 1904.

Vincetoxicum calcicola (Greenm.) Standl. Contr. U.S. Nat. Herb. **23**: 1191. 1924.

MATELEA **congesta** (Dcne.) Woodson, comb. nov.

Gonolobus congestus Dcne. in DC. Prodr. **8**: 597. 1844.

Vincetoxicum congestum (Dcne.) Standl. Contr. U.S. Nat. Herb. **23**: 1189. 1924.

MATELEA **congestiflora** (Donn.Sm.) Woodson, comb. nov.

Cynanchum hirsutum Sesse & Mociño, Fl. Mex. 76. 1887, non Vell.

Macroscepis congestiflora Donn.Sm. Bot. Gaz. **25**: 149. 1898.

MATELEA **diademata** (Edwards) Woodson, comb. nov.

Gonolobus diadematus Edwards, Bot. Reg. **3:** *pl.252.* 1817.

Vincetoxicum diadematum (Edwards) Standl. Contr. U.S. Nat. Herb. **23:** 1188. 1924.

MATELEA **magnifolia** (Pittier) Woodson, comb. nov.

Gonolobus magnifolius Pittier, Contr. U.S. Nat. Herb. **13:** 104. *fig.13.* 1910.

Vincetoxicum magnifolium (Pittier) Standl. loc. cit. **23:** 1188. 1924.

MATELEA **obovata** (HBK.) Woodson, comb. nov.

Macroscepis obovata HBK. Nov. Gen. **3:** 200. 1819.

SUBGENUS 4. TRICHOSACME

MATELEA **lanata** (Zucc.) Woodson, comb. nov.

Trichosacme lanata Zucc. Abh. Akad. Wiss. Munchen **4²:** 11. 1845.

An explanation, if not an apology, is in order for reducing *Trichosacme* from generic status. *M. lanata* is quite unmistakable because of the copius lanate pubescence and long plumose corolla lobes; but aside from these particulars it is manifestly intermediate between other groups, having somewhat the corona of *Chthamalia,* the pollinia of *Ibatia,* and the corolla (except the lobe appendages) of a miniature *Macroscepis.*

SUBGENUS 5. POICILLA

MATELEA **ovatifolia** (Griseb.) Woodson, comb. nov.

Poicilla ovatifolia Griseb. Cat. Pl. Cub. 177. 1866.

Ptychanthera ovatifolia (Griseb.) Schltr. in Urb. Symb. Ant. **1:** 279. 1899.

MATELEA **tamnifolia** (Griseb.) Woodson, comb. nov.

Poicilla tamnifolia Griseb. Cat. Pl. Cub. 176. 1866.

SUBGENUS 6. PTYCANTHERA

§. *Pauciflorae*

MATELEA **acuminata** (Griseb.) Woodson, comb. nov.

Orthosia acuminata Griseb. Cat. Pl. Cub. 175. 1866.

Ptychanthera Berterii acc. to Schltr. in Urb. Symb. Ant. **1:** 279. 1899, non Dcne.

Poicilla acuminata (Griseb.) Schltr. loc. cit. **5**: 469.
1908.

Poicillopsis acuminata (Griseb.) Schltr. loc. cit. **7**: 339.
1912.

MATELEA **nipensis** (Urb.) Woodson, comb. nov.

Gonolobus nipensis Urb. Symb. Ant. **9**: 421. 1925.

MATELEA **oblongata** (Griseb.) Woodson, comb. nov.

Orthosia oblongata Griseb. Cat. Pl. Cub. 176. 1866.

Ptychanthera oblongata (Griseb.) Schltr. in Urb. Symb.
Ant. **1**: 280. 1899.

Poicilla oblongata (Griseb.) Schltr. loc. cit. **5**: 470.
1908.

Poicillopsis oblongata (Griseb.) Schltr. loc. cit. **7**: 339.
1912.

MATELEA **pauciflora** (Spreng.) Woodson, comb. nov.

Gonolobus pauciflorus Spreng. Syst. **1**: 846. 1825.

Ptycanthera Berterii Dcne. in DC. Prodr. **8**: 606. 1844,
not acc. to Schltr. in Urb. Symb. Ant. **1**: 279. 1899.

§. *Variifoliae*

MATELEA **bayatensis** (Urb.) Woodson, comb. nov.

Gonolobus bayatensis Urb. Symb. Ant. **9**: 420. 1925.

MATELEA **Ekmanii** (Urb.) Woodson, comb. nov.

Gonolobus Ekmanii Urb. Symb. Ant. **9**: 422. 1925.

MATELEA **Sintenisii** (Schltr.) Woodson, comb. nov.

Gonolobus Sintenisii Schltr. in Urb. Symb. Ant. **1**: 288.
1899.

Vincetoxicum Sintenisii (Schltr.) Britton, Sci. Surv.
Porto Rico & Virgin Isl. **6**: 100. 1925.

MATELEA **tigrina** (Griseb.) Woodson, comb. nov.

Gonolobus tigrinus Griseb. Pl. Wright. 520. 1862.

MATELEA **variifolia** (Schltr.) Woodson, comb. nov.

Gonolobus variifolius Schltr. in Urb. Symb. Ant. **1**: 286.
1899.

Vincetoxicum variifolium (Schltr.) Britton, Sci. Surv.
Porto Rico & Virgin Isl. **6**: 100. 1925.

The subgenus *Ptycanthera* was largely the deciding factor
in the inclusive treatment of *Matelea* which I have adopted.

Were it not for the Antillean species, one might compose a fairly respectable key to several genera upon the continent, following generally the lines of the key to subgenera and sections of *Matelea* as it now appears. However, the Antillean species cut so sharply across most of the distinctions between the continental groups that the only way I can distinguish them from the latter in print is by the geographical factor. Were it not for their ambiguity with respect to the continental entities, one might obliterate *Ptycanthera* entirely, distributing §. *Pauciflorae* and §. *Variifoliae,* perhaps, to the continental subgenera *Eumatelea* and *Heliostemma* respectively.

Variation of the corona in *Ptycanthera* appears largely to be responsive to the development of the anther head stipe. Where the latter is fairly pronounced, in § *Pauciflorae,* the corona adopts much the same fluted appearance with subtending skirt as in *Eumatelea* § *Reticulatae;* but where the anther head is sessile (§ *Variifoliae),* the corona becomes a rotate disc as in *Heliostemma,* or a shallow 5-angled ring, in either case with 5 partitions, bosses, or hooks corresponding to the fluted buttresses of § *Pauciflorae.* In *M. Sintenisii* the compression of the anther head and corona apparently has led to the formation by the corolla throat of a rather prominent faucal annulus. The anther and pollinium structures are somewhat more variable even than in the continental species.

Yet, withal, the superficial aspect of the various species is so similar in most cases that I cannot but view them as extremely closely related, particularly in view of their restricted geographical distribution. The exasperations attendant upon their attempted segregation are illustrated graphically by Schlechter's vacillation between *Poicilla, Ptycanthera* (spelled *Ptychanthera* by him), *Poicillopsis,* and *Gonolobus,* with the familiar *Vincetoxicum-motif* supplied by Dr. Britton.

SUBGENUS 7. CHTHAMALIA

MATELEA **adenocardium** (Standl.) Woodson, comb. nov.
    Vincetoxicum adenocardium Standl. Field Mus. Publ. Bot.
      17: 267. 1937.
MATELEA **Baldwyniana** (Sweet) Woodson, comb. nov.

Gonolobus Baldwynianus Sweet, Hort. Brit. ed.2. 360. 1830.

Vincetoxicum Baldwinianum (Sweet) Britton, Mem. Torrey Club **5**: 265. 1894.

Odontostephana Baldwiniana (Sweet) Alexander, in Small, Man. Fl. 1077. 1933.

MATELEA **biflora** (Raf.) Woodson, comb. nov.

Gonolobus biflorus Raf. New Fl. N. Amer. **4**: 58. 1836.

Chthamalia biflora (Raf.) Dcne. in DC. Prodr. **8**: 605. 1844.

Vincetoxicum biflorum (Raf.) Heller, Contr. Herb. Franklin & Marshall Coll. **1**: 79. 1895.

MATELEA **brevicoronata** (Robins.) Woodson, comb. nov.

Gonolobus parviflorus var. *brevicoronatus* Robins. Proc. Amer. Acad. **26**: 169. 1891.

MATELEA **camporum** (Brandg.) Woodson, comb. nov.

Vincetoxicum camporum Brandg. Univ. Calif. Publ. Bot. **4**: 185. 1911.

MATELEA **carolinensis** (Jacq.) Woodson, comb. nov.

Cynanchum carolinense Jacq. Coll. **2**: 288. 1788.

Gonolobus carolinensis (Jacq.) R.Br. Mem. Wern. Soc. **1**: 35. 1809.

Vincetoxicum carolinense (Jacq.) Britton, Mem. Torrey Club **5**: 265. 1894.

Odontostephana carolinensis (Jacq.) Alexander, in Small, Man. Fl. 1077. 1933.

MATELEA **cynanchoides** (Engelm.) Woodson, comb. nov.

Gonolobus cynanchoides Engelm. in Engelm. & Gray, Boston Journ. Nat. Hist. **5**: 251. 1845.

Vincetoxicum cynanchoides (Engelm.) Heller, Muhlenbergia **1**: 2. 1900.

MATELEA **decipiens** (Alexander) Woodson, comb. nov.

Odontostephana decipiens Alexander, in Small, Man. Fl. 1077. 1933.

Gonolobus decipiens (Alexander) Perry, Rhodora **40**: 286. 1938.

MATELEA **flavidula** (Chapm.) Woodson, comb. nov.

Gonolobus flavidulus Chapm. Bot. Gaz. **3**: 12. 1878.

Gonolobus hirsutus var. *flavidulus* (Chapm.) A.Gray, Syn.
Fl. ed.2, 2^1: 404. 1886.

Vincetoxicum flavidulum (Chapm.) Heller, Muhlenbergia
1: 2. 1900.

Odontostephana flavidula (Chapm.) Alexander, in Small,
Man. Fl. 1078. 1933.

MATELEA **floridana** (Vail) Woodson, comb. nov.

Vincetoxicum floridanum Vail, Bull. Torrey Club **26**: 428.
1899.

Odontostephana floridana (Vail) Alexander, in Small,
Man. Fl. 1078. 1933.

MATELEA **Greggii** (Vail) Woodson, comb. nov.

Vincetoxicum Greggii Vail, Bull. Torrey Club **26**: 431.
1899.

MATELEA **LeSueurii** (Standl.) Woodson, comb. nov.

Vincetoxicum LeSueurii Standl. Field Mus. Publ. Bot. **17**:
270. 1937.

The pollinia of this species are not the subquadrate-reniform
sort typical of *Chthamalia,* but are more nearly triangular-
pyriform. Nevertheless, the affinities of *M. LeSueurii* unmis-
takably are with that subgenus, particularly with *M. Num-
mularia.*

MATELEA **Nummularia** (Dcne.) Woodson, comb. nov.

Chthamalia Nummularia Dcne. in DC. Prodr. **8**: 605.
1844.

MATELEA **obliqua** (Jacq.) Woodson, comb. nov.

Cynanchum obliquum Jacq. Coll. **1**: 148. 1786.

Gonolobus obliquus (Jacq.) R.Br. Mem. Wern. Soc. **1**: 35.
1809.

Vincetoxicum obliquum (Jacq.) Britton, Mem. Torrey
Club **5**: 266. 1894.

Odontostephana obliqua (Jacq.) Alexander, in Small,
Man. Fl. 1077. 1933.

MATELEA **parviflora** (Torr.) Woodson, comb. nov.

Lachnostoma (?) parviflorum Torr. Rept. Bot. Mex.
Bound. Surv. 165. 1859.

Gonolobus parviflorus (Torr.) A.Gray, Proc. Amer. Acad.
12: 79. 1877.

Vincetoxicum parviflorum (Torr.) Heller, Muhlenbergia
    1: 2. 1900.

MATELEA **parvifolia** (Torr.) Woodson, comb. nov.

Gonolobus parvifolius Torr. Rept. Bot. Mex. Bound. Surv.
    166. 1859.

Gonolobus hastulatus A.Gray, Proc. Amer. Acad. **12**: 78.
    1877.

Vincetoxicum hastulatum (A.Gray) Heller, Muhlenbergia
    1: 2. 1900.

Gonolobus californicus Jepson, Man. 771. 1925.

MATELEA **pedunculata** (Dcne.) Woodson, comb. nov.

Chthamalia pedunculata Dcne. in DC. Prodr. **8**: 605. 1844.

MATELEA **producta** (Torr.) Woodson, comb. nov.

Gonolobus productus Torr. Rept. Bot. Mex. Bound. Surv.
    165. 1859.

Vincetoxicum productum (Torr.) Vail, Bull. Torrey Club
    26: 431. 1899.

MATELEA **prostrata** (Willd.) Woodson, comb. nov.

Cynanchum prostratum Willd. Sp. Pl. **1**: 1257. 1798.

Gonolobus prostratus (Willd.) R.Br. Mem. Wern. Soc.
    1: 35. 1809.

Lachnostoma prostratum (Willd.) Dcne. in DC. Prodr. **8**:
    602. 1844.

Tetracustelma prostrata (Willd.) Baill. Hist. Pl. **10**: 292.
    1891.

MATELEA **pubiflora** (Dcne.) Woodson, comb. nov.

Chthamalia pubiflora Dcne. in DC. Prodr. **8**: 605. 1844.

Gonolobus pubiflorus (Dcne.) Engelm. in Engelm. & Gray,
    Boston Journ. Nat. Hist. **5**: 252. 1845.

Vincetoxicum pubiflorum (Dcne.) Heller, Muhlenbergia **1**:
    2. 1900.

Edisonia pubiflora (Dcne.) Small, Man. Fl. 1078. 1933.

MATELEA **Schaffneri** (A.Gray) Woodson, comb. nov.

Gonolobus Schaffneri A.Gray, in Hemsl. Biol. Centr.-Am.
    Bot. **2**: 334. 1882; A.Gray, Proc. Amer. Acad. **21**: 399.
    1886.

Gonolobus bifidus Hemsl. Biol. Centr.-Amer. Bot. **2**: 330.
    1882.

MATELEA **Shortii** (A.Gray) Woodson, comb. nov.

Gonolobus obliquus var. *Shortii* A.Gray, Syn. Fl. 2¹: 104.
1878.

Vincetoxicum Shortii (A.Gray) Britton, Mem. Torrey
Club **5**: 266. 1894.

Gonolobus Shortii A.Gray, Bot. Gaz. **8**: 191. 1883.

Odontostephana Shortii (A.Gray) Alexander, in Small,
Man. Fl. 1077. 1933.

MATELEA **stenopetala** (A.Gray) Woodson, comb. nov.

Gonolobus stenopetalus A.Gray, Proc. Amer. Acad. **21**:
398. 1886.

Vincetoxicum stenopetalum (A.Gray) Standl. Contr. U.S.
Nat. Herb. **23**: 1190. 1924.

MATELEA **Vailiana** Woodson, nom. nov.

Gonolobus acuminatus A.Gray, Proc. Amer. Acad. **21**:
399. 1886, non *Matelea acuminata* (Griseb.) Woodson.

Vincetoxicum acuminatum (A.Gray) Vail, Bull. Torrey
Club **26**: 431. 1899.

MATELEA **Wootonii** (Vail) Woodson, comb. nov.

Vincetoxicum Wootonii Vail, Bull. Torrey Club **28**: 485.
pl.30. 1901.

This is the characteristic group of *Matelea* in northern
Mexico and the southern United States. The pollinia are well
illustrated for the species "in the Manual Range" by Miss
Perry (Rhodora **40**: *pl.494.* 1938) where the contrasting fea-
tures of true *Gonolobus* pollinia are shown also. I believe that
Chthamalia is perhaps most closely related to *Ibatia* amongst
the subgenera of *Matelea,* the "pendulous" pollinia of the
latter frequently appearing much like the "horizontal" pol-
linia of the former (merely of greater vertical dimension).
The corona of the two subgenera, also, are much alike, but the
internal ligules of the former are merely adnate (sometimes
nearly free) to the outer segments, whereas the fusion is virtu-
ally complete in the latter.

SUBGENUS 8. PHEROTRICHIS

MATELEA **Balbisii** (Dcne.) Woodson, comb. nov.

Asclepias villosa Balb. Mem. Accad. Sci. Torino **7**: 386. 1803, non Mill.

Cynanchum villosum (Balb.) R. & S. Syst. **6**: 103. 1819.

Lachnostoma Balbisii Dcne. in DC. Prodr. **8**: 602. 1844.

Gonolobus pogonanthus Hemsl. Biol. Centr.-Am. Bot. **2**: 333. 1882.

Pherotrichis Balbisii (Dcne.) A.Gray, Proc. Amer. Acad. **21**: 400. 1886; Syn. Fl. ed.2. **2**¹: 462. 1886.

Pherotrichis Schaffneri A.Gray, loc. cit. 1886.

MATELEA **chihuahuensis** (A.Gray) Woodson, comb. nov.

Gonolobus chihuahuensis A.Gray, Proc. Amer. Acad. **21**: 398. 1886.

Vincetoxicum chihuahuense (A.Gray) Standl. Field Mus. Publ. Bot. **17**: 270. 1937.

MATELEA **leptogenia** (Robins.) Woodson, comb. nov.

Pherotrichis leptogenia Robins. Proc. Amer. Acad. **29**: 319. 1894.

SUBGENUS 9. AMPHORELLA

MATELEA **castanea** (Brandg.) Woodson, comb. nov.

Amphorella castanea Brandg. Univ. Calif. Publ. Bot. **4**: 92. 1910.

SUBGENUS 10. TIARASTEMMA

MATELEA **calcarata** Woodson, comb. nov.

Vincetoxicum calcaratum Woodson, Amer. Journ. Bot. **22**: 689. *pl.1. fig.8.* 1935.

MATELEA **belizensis** (Lundell & Standl.) Woodson, comb. nov.

Vincetoxicum belizense Lundell & Standl. in Standl. Field Mus. Publ. Bot. **17**: 268. 1937.

SUBGENUS 11. POLYSTEMMA

MATELEA **Decaisnei** Woodson, nom. nov.

Polystemma viridiflora Dcne. in DC. Prodr. **8**: 602. 1844, non *M. viridiflora* (G.F.W.Mey.) Woodson.

MATELEA **rupestris** (Brandg.) Woodson, comb. nov.

Polystemma rupestre Brandg. Univ. Cal. Publ. Bot. **7**: 330. 1920.

MATELEA **scopulorum** (Brandg.) Woodson, comb. nov.

Polystemma scopulorum Brandg. Univ. Calif. Publ. Bot.
6: 189. 1915.

SUBGENUS 12. HELIOSTEMMA

MATELEA **caudata** (A.Gray) Woodson, comb. nov.

Gonolobus caudatus A.Gray, Proc. Amer. Acad. 21: 399.
1886.

Vincetoxicum caudatum (A.Gray) Standl. Contr. U.S.
Nat. Herb. 23: 1190. 1924.

MATELEA **crenata** (Vail) Woodson, comb. nov.

Vincetoxicum crenatum Vail, Bull. Torrey Club 26: 429.
1899.

This species might almost as well be placed in *Ibatia* upon
the basis of the pollinia alone, for they are only slightly falci-
form. The corona segments, also, are scarcely typical of *Helio-
stemma* in that they are not strongly adnate to the corolla
throat. However, they do have a conspicuous internal boss
which is characteristic of the latter subgenus and never found
in the former.

MATELEA **cyclophylla** (Standl.) Woodson, comb. nov.

Vincetoxicum cyclophyllum Standl. Contr. U.S. Nat. Herb.
23: 1191. 1924.

MATELEA **nigrescens** (Schlecht.) Woodson, comb. nov.

Gonolobus nigrescens Schlecht. Linnaea 8: 522. 1833.

Vincetoxicum nigrescens (Schlecht.) Standl. Contr. U.S.
Nat. Herb. 23: 1192. 1924.

MATELEA **picturata** (Hemsl.) Woodson, comb. nov.

Gonolobus picturatus Hemsl. Biol. Centr.-Am. Bot. 2:
332. 1882.

MATELEA **pilosa** (Benth.) Woodson, comb. nov.

Gonolobus pilosus Benth. Pl. Hartw. 289. 1848.

Gonolobus atratus A.Gray, Proc. Amer. Acad. 22: 436.
1887.

Gonolobus suberiferus Robins. Proc. Amer. Acad. 27:
181. 1892.

Vincetoxicum Grayanum Standl. Contr. U.S. Nat. Herb.
23: 1191. 1924.

Vincetoxicum pilosum (Benth.) Standl. loc. cit. 1924.

Vincetoxicum suberiferum (Robins.) Standl. loc. cit. 1189.
1924.

Vincetoxicum quercetorum Standl. Field Mus. Publ. Bot.
17: 271. 1937.

MATELEA **Pittieri** (Standl.) Woodson, comb. nov.

Vincetoxicum Pittieri Standl. Field Mus. Publ. Bot. **17**:
270. 1937.

Vincetoxicum discolor Woodson, Ann. Missouri Bot. Gard.
25: 833. *fig.1*. 1938.

SUBGENUS 13. EUMATELEA

§. *Reticulatae*

MATELEA **alabamensis** (Vail) Woodson, comb. nov.

Vincetoxicum alabamense Vail, Bull. Torrey Club **30**:
178. *pl.9*. 1903.

MATELEA **campechiana** (Standl.) Woodson, comb. nov.

Vincetoxicum campechianum Standl. Carnegie Inst.
Wash. Publ. 461: 82. 1935.

MATELEA **Gentlei** (Lundell & Standl.) Woodson, comb. nov.

Vincetoxicum Gentlei Lundell & Standl. Field Mus.
Publ. Bot. **17**: 269. 1937.

MATELEA **lanceolata** (Dcne.) Woodson, comb. nov.

Gonolobus lanceolatus Dcne. in DC. Prodr. **8**: 598. 1844.

Vincetoxicum stenophyllum Standl. Contr. U.S. Nat.
Herb. **23**: 1188. 1924.

MATELEA **reticulata** (Engelm.) Woodson, comb. nov.

Gonolobus reticulatus Engelm. ex A.Gray, Proc. Amer.
Acad. **12**: 75. 1877.

Vincetoxicum reticulatum (Engelm.) Heller, Bot. Expl.
Texas, 79. 1895.

MATELEA **Tuerckheimii** (Donn.Sm.) Woodson, comb. nov.

Gonolobus Tuerckheimii Donn. Sm. Bot. Gaz. **44**: 116.
1907.

Vincetoxicum trichoneuron Standl. ex Yuncker, Field
Mus. Publ. Bot. **17**: 388. 1938.

MATELEA **velutina** (Schlecht.) Woodson, comb. nov.

Gonolobus velutinus Schlecht. Linnaea **8**: 521. 1833.

Vincetoxicum velutinum (Schlecht.) Standl. Contr. U.S.
Nat. Herb. **23**: 1189. 1924.

§. *Pseudobarbatae*

MATELEA **guatemalensis** (K.Sch.) Woodson, comb. nov.
Gonolobus velutinus var. *calycinus* Donn.Sm. Bot. Gaz.
13: 189. 1888.
Gonolobus guatemalensis K.Sch. in Engl. & Prantl, Nat.
Pflanzenfam. **4²**: 302. 1895.

MATELEA **pinguifolia** (Standl.) Woodson, comb. nov.
Vincetoxicum pinguifolium Standl. Journ. Wash. Acad.
Sci. **17**: 13. 1927.

MATELEA **pseudobarbata** (Pittier) Woodson, comb. nov.
Gonolobus pseudobarbatus Pittier, Contr. U.S. Nat.
Herb. **13**: 105. *fig.14.* 1910.

Matelea nigrescens shows a strong affinity with this section,
but has been placed in *Heliostemma* because of its falciform
pollinia.

§. *Viridiflorae*

MATELEA **grandiflora** (Standl.) Woodson, comb. nov.
Vincetoxicum grandiflorum Standl. Carnegie Inst.
Wash. Publ. 461: 83. 1935.

MATELEA **viridiflora** (G.F.W.Mey.) Woodson, comb. nov.
Cynanchum viridiflorum G.F.W.Mey. Prim. Fl. Esseq.
141. 1818.
Gonolobus viridiflorus (G.F.W.Mey.) R. & S. Syst. **6**:
61. 1819.
Vincetoxicum viridiflorum (G.F.W.Mey.) Standl.
Contr. U.S. Nat. Herb. **27**: 311. 1928.

This little group illustrates the maddening complications
that result from attempts at segregation in the Gonolobeae.
M. viridiflora and *M. grandiflora* quite obviously are very
closely related, as evidenced particularly by the interrupted
corolline annulus. Other characters, however, point strongly
to relationship with other groups of *Matelea,* with the excep-
tion of the pollinia, which are scarcely similar to those of
Eumatelea, and can be construed as "triangular-pyriform"

only with a considerable stretch of the imagination. But on the other hand, the pollinia of the two species are so dissimilar that I can find no descriptive term to cover both, and at the same time to distinguish them from *Eumatelea*.

SUBGENUS 14. MICRODACTYLON

MATELEA **cordata** (Brandg.) Woodson, comb. nov.
  Microdactylon cordatum Brandg. Zoe **5**: 252. 1908.

SUBGENUS 15. PACHYSTELMA

MATELEA **bicolor** (Britton & Wilson) Woodson, comb. nov.
  Marsdenia bicolor Britton & Wilson, Bull. Torrey Club **50**: 47. 1923.
  Gonolobus bicolor (Britton & Wilson) Urb. Symb. Ant. **9**: 421. 1925.
MATELEA **crassifolia** (Standl.) Woodson, comb. nov.
  Vincetoxicum crassifolium Standl. Field Mus. Publ. Bot. **8**: 36. 1930.
MATELEA **megacarpha** (Brandg.) Woodson, comb. nov.
  Vincetoxicum megacarphum Brandg. Univ. Cal. Publ. Bot. **4**: 381. 1913.
  Pachystelma cordatum Brandg. loc. cit. **7**: 330. 1920.
  Dictyanthus brachistanthus Standl. Field Mus. Publ. Bot. **8**: 38. 1930.

SUBGENUS 16. DICTYANTHUS

MATELEA **altatensis** (Brandg.) Woodson, comb. nov.
  Gonolobus altatensis Brandg. Zoe **5**: 244. 1908.
MATELEA **ceratopetala** (Donn.Sm.) Woodson, comb. nov.
  Dictyanthus ceratopetalus Donn.Sm. Bot. Gaz. **18**: 208. 1893.
MATELEA **dictyantha** Woodson, nom. nov.
  Rytidoloma reticulata Turcz. Bull. Soc. Nat. Mosc. **25²**: 320. 1852, non *Matelea reticulata* (Engelm.) Woodson.
  Dictyanthus reticulatus (Turcz.) Benth. & Hook. Gen. Pl. **2**: 765. 1876.
MATELEA **diffusa** Woodson, nom. nov.
  Dictyanthus prostratus Brandg. Univ. Cal. Publ. Bot. **7**: 329. 1920, non *Matelea prostrata* (Willd.) Woodson.

MATELEA **Hemsleyana** Woodson, nom. nov.

Dictyanthus parviflorus Hemsl. Biol. Centr. Am. Bot. **2:**
329. 1882, non Matelea parviflora (Torr.) Woodson.

MATELEA **Pavonii** (Dcne.) Woodson, comb. nov.

Dictyanthus Pavonii Dcne. in DC. Prodr. **8:** 605. 1844.

Tympananthe suberosa Hassk. Flora **30:** 758. 1847.

MATELEA **Standleyana** Woodson, nom. nov.

Dictyanthus tigrinus Conzatti & Standl. in Standl. Contr.
U.S. Nat. Herb. **23:** 1183. 1924, non Matelea tigrina
(Griseb.) Woodson.

MATELEA **stapeliaeflora** (Reichb.) Woodson, comb. nov.

Dictyanthus stapeliaeflora Reichb. Sel. Sem. Hort. Dres-
den, 4. 1850.

MATELEA **tuberosa** (Robins.) Woodson, comb. nov.

Dictyanthus tuberosus Robins. Proc. Amer. Acad. **27:** 180.
1892.

MATELEA **yucatanensis** (Standl.) Woodson, comb. nov.

Dictyanthus yucatanensis Standl. Field Mus. Publ. Bot. **8:**
37. 1930.

Dictyanthus aeneus Woodson, Amer. Journ. Bot. **22:** 691.
1935.

I am very reluctant to merge *Dictyanthus* with *Matelea*,
since the various species here show considerably more coher-
ence and distinction than in other generic groups. However,
generic lines cannot be drawn sharply due to such groups as
Pachystelma, Labidostelma, and *Macroscepis*. The only really
unique feature of *Dictyanthus* is that the faucal callus, or an-
nulus, of the corolla is digitate, as are the segments of the
corona. I am prepared for vigorous opposition from those
who are accustomed to think of *Dictyanthus* as exemplified by
D. Pavonii. *M. altatensis* provides a very suggestive link with
either *Pachystelma* or *Eumatelea*, according to one's view-
point at a particular time.

VII. FISCHERIA DC. Cat. Hort. Monsp. 112. 1813.

I am maintaining *Fischeria* with misgivings, and only pro-
visionally, since its affinities with the broad interpretation of

Matelea are unmistakable, as shown particularly in the pollinium structure and the mixed indument with interspersed bulbose, glandular hairs. In the Central American species the corona appears outstanding, but is scarcely different from that of *Eumatelea* § *Pseudobarbatae*. The anthers, also, show the inflated vesicular development mentioned in the key to genera. But in *F. viridis* Moldenke, recently discovered in Colombia, the corona is resolved into a more typical structure for *Matelea,* and the anthers are not vesicular. Should more species comparable to *F. viridis* appear in the rich South American flora, it is difficult to foresee what characters could be found to support the genus other than the crisped corolla lobes. Since *Fischeria* is not well represented in North America, the species there being quite easily distinguished, I am leaving the question of its validity until I am more familiar with the South American congeners.

VIII. GONOLOBUS Michx. Fl. Bor. Am. **1**: 119. 1803.

Vincetoxicum Walt. Fl. Carol. 13, 104. 1788, non Moench.
Fimbristemma Turcz. Bull. Soc. Nat. Mosc. **25²**: 320. 1852.
Exolobus Fourn. in Mart. Fl. Bras. **6⁴**: 318. 1885.
Trichostelma Baill. Hist. Pl. **10**: 287. 1891.
Lachnostoma of North American authors.

The complications concerning the use of *Gonolobus* Michx. and *Vincetoxicum* Walt., the "temporary" conservation of *Vincetoxicum* Moench. over the latter, and the typification of *Gonolobus* by *G. gonocarpos* (Walt.) Perry have been discussed in previous paragraphs (p. 213). It may be remembered that the original element of *Vincetoxicum* Walt. (or *Gonolobus,* through the rejection of the earlier name) consists of two species, *G. gonocarpos* (Walt.) Perry, the type, and *G. carolinensis* (Jacq.) Schultes *(V. acanthocarpos* Walt.). Until recently no question has been raised against the consideration of these two species as congeneric, and *Gonolobus* became the general catch-all for gonoloboid species without sufficiently striking innovations of the corona to prompt their

designation as separate genera. At about the opening of the
present century, however, the earlier *Vincetoxicum* Walt. was
revived by Dr. Britton and Miss Vail at the New York Botani-
cal Garden. Transfers from *Gonolobus* were then in order,
and few species of the complex have been described for that
genus since. It seems rather severe that American botanists
now will have to adjust themselves anew to the conservation
of the dubiously valid *Vincetoxicum* Moench of Europe.

In 1933 (in Small, Man. Fl. 1076.) E. J. Alexander separated
G. gonocarpos and *G. carolinensis* generically, founding the
genus *Odontostephana* with the latter, together with other
species from the southeastern United States. Alexander quite
naturally used *Vincetoxicum* Walt. in place of *Gonolobus,* the
judgment of the authorities at Kew not yet having been passed.
The key characters used to separate *Vincetoxicum* from
Odontostephana were taken from the coronas, whether
"Crown disk-like or saucer shaped, obscurely if at all ridged,"
or "Crown cup-shaped or incurved at the tip, usually crested or
appendaged on the inner side." In the descriptions of the two
genera, attention was called also to the characters of the fruits,
longitudinally winged in the former, and muricate in the latter,
as observed by Walter in 1788. It is regrettable that *Odonto-
stephana* is antedated by *Tetracustelma* Baill. if a narrow
generic concept is adopted, and that a broad concept will sub-
merge it in *Matelea* Aubl.

I have tried in vain to find characters of the corona which
will separate *Gonolobus* and *Matelea,* but the structures of the
anthers of the two genera appear to me as amply sufficient for
distinction. The anthers of both vary considerably in size, po-
sition relative to the anther head, hyaline apical appendage,
and nature of the marginal "wings." But in the species that
I have assigned to *Gonolobus* the anther proper bears a more
or less conspicuous, fleshy, usually laminate dorsal appendage
which I never have found indicated to any degree in species
assigned to *Matelea.* These dorsal appendages vary greatly
from species to species, and although rather poorly developed
as a rule in the temperate representatives, are very conspicu-

ous in the tropics. Typically, they are somewhat reniform in outline, but frequently deeply 2-lobed or entire, and rarely cleft into three divisions. The dorsal anther appendages are indicated in Alexander's figure for *Vincetoxicum* Walt. (loc. cit. 1933), although their significance is not mentioned, and a splendid illustration of them is provided by Baillon (Hist. Pl. **10**: 235. *fig.177*. 1891) for *G. erianthus*.

The dorsal anther appendages of *Gonolobus* have been over-looked in most species of North America, but they were made the chief foundation for the genus *Exolobus* by Fournier (cf. Mart. Fl. Bras. **6**⁴: *pl.94*. 1885), who designated them as *"corona superior."* The species assigned to *Gonolobus* by Fournier all are of the element represented by *G. hirsutus* Michx. which I am relegating to *Matelea*. K. Schumann (in Engl. & Prantl, Nat. Pflanzenfam. **4**²: 298, 301–302. 1895) followed Fournier in the separation of *Gonolobus* and *Exolobus*, but appears to have been remarkably confused, for the dorsal anther appendages of my terminology are described as "inner corona" ("corona . . . innere an den A. befestigt, nach aussen strahlend, fleischig.") for the former, but for the latter simply as appendages of the anthers ("Stb. mit einem mittleren, fleischigen, nach aussen gerichteten Fortsatze. . .").

As I have explained previously (p. 199), flowers of *Gonolobus* as interpreted in this paper customarily have three structures which may be called "corona" if the terminology is loose: a corolline faucal annulus, frequently ciliate, a fleshy true corona borne at the base of the staminal column, and the dorsal appendages of the anthers proper. In his key to the Gonolobeae, Schumann (loc. cit. 298) places both *Gonolobus* and *Exolobus* under the division "II. Corona doppelt," and distinguishes them by "1. Äussere Corona kahl" and "2. Äussere Corona gewimpert," respectively, apparently referring to the corolline annulus.

In his descriptions of the two genera, however, Schumann reveals by his ambiguity how confused was his concept: "Corona ringförmig, einfach oder doppelt, die äussere zuweilen noch von einem häutigen Rande umgeben, so dass man fast 3

Coronen unterscheiden kann, oft ringförmig, der Blkr. an-
geheftet, kurz, gestutzt oder gelappt, zuweilen durch 5 Gewebe-
platten mit dem Gynostegium verbunden; innere an den A.
befestigt, nach aussen strahlend, fleischig'' *(Gonolobus,* p.
301); ''Corona doppelt: äussere in der Form eines sehr nied-
rigen, behaarten, aus den Blkr. vortretenden Ringes, die
innere aus 5 freien Schuppen bestehend, welche der Röhre des
Gynostegiums angeheftet sind. Stb. mit einem mittleren,
fleischigen, nach aussen gerichteten Fortsatze und einem
häutigen Mittelbandanhang'' *(Exolobus,* p.302). The *coup de
grace* is given these verbal circumlocutions by a consideration
of *fig. 92, N–T,* provided by Schumann (p.301) to illustrate
Gonolobus and *Exolobus.* The floral structures are found to be
equivalent in all important particulars, even to a ''gewimpert
corona'' (ciliate corolline annulus) for *G. riparius.*

The extended quotations from Schumann should be suffi-
cient to illustrate the ambiguity that results from treating
the term ''corona'' in a complex sense. The dorsal anther ap-
pendages of *Gonolobus* are not equivalent to any structure
found in *Matelea.* At one time during these studies, I suspected
that they might represent the adnation to the anther of the
inner ligules commonly accompanying the corona segments of
the latter genus. This is shown to be erroneous, however, by
the fact that these ligules almost invariably occur in *Gonol-
obus* in addition to the dorsal anther appendages, which ap-
parently are more directly comparable to the vesicular tissue
of the anthers of *Fischeria.*

I am not yet sufficiently informed to know positively what
will result when this character is applied extensively to the
South American gonoloboids, but wide observations indicate
its validity. Supporting characters are found amongst the
relatively few species of *Gonolobus* and *Matelea* for which
fruit is known, the follicles of the former being longitudinally
winged, infrequently quite smooth, and those of the latter
muricate or infrequently smooth. The smooth condition would
appear to be derived from both series. In *Matelea,* as has been
explained previously, a peculiar indument of eglandular and

interspersed glandular hairs characteristically occurs; such an indument never is found in *Gonolobus*.

Amongst the North American species of *Gonolobus* with which I am familiar at present, the following divisions into subgenera appear both natural and convenient. As usual, I have illustrated them with necessary transfers.

KEY TO SUBGENERA

A. Corolla with widely spreading or reflexed lobes, with a more or less pro-
     nounced faucal annulus exterior to the true corona.
  B. Anthers only about half included beneath the broadly 5-gonal stigma
     head ....1. PTEROLOBUS
  BB. Anthers wholly (except the dorsal appendages) included beneath the
     saliently 5-gonal stigma head......................2. EUGONOLOBUS
AA. Corolla with erect or ascending lobes, without a faucal annulus..........
     ....3. PSEUDOLACHNOSTOMA

I should like to include *Trichostelma* Baill. in this key either as a subgenus or as a section under *Eugonolobus,* but the height of the corolline annulus appears to be far too variable.

SUBGENUS 1. PTEROLOBUS

    GONOLOBUS **chiapensis** (Brandg.) Woodson, comb. nov.
      Vincetoxicum chiapense Brandg. Univ. Cal. Publ. Bot. **6:**
      190. 1915.

In addition to the preceding, *Pterolobus* includes such species as *G. niger* R.Br., *G. Salvinii* Hemsl., and *G. nemorosus* Dcne. The name refers to the undulated wings of the follicles of the few species where I have observed them.

SUBGENUS 2. EUGONOLOBUS

    GONOLOBUS **albomarginatus** (Pittier) Woodson, comb. nov.
      Exolobus albomarginatus Pittier, Contr. U.S. Nat. Herb.
      13: 108. *fig.16.* 1910.
    GONOLOBUS **aristolochiaefolius** (Brandg.) Woodson, comb.
    nov.
      Fischeria aristolochiaefolia Brandg. Univ. Cal. Publ. Bot.
      6: 190. 1915.
    GONOLOBUS **calycosus** (Donn.Sm.) Woodson, comb. nov.
      Trichostelma ciliatum Baill. Hist. Pl. **10:** 288. 1891, non
      G. ciliatus Schltr.

Fimbristemma calycosa Donn.Sm. Bot. Gaz. **16**: 196. *pl.
16.* 1891.

Gonolobus **cteniophorus** (Blake) Woodson, comb. nov.
  Vincetoxicum cteniophorum Blake, Contr. Gray Herb. 52:
  84. 1917.
  Vincetoxicum ? tortum Brandg. Univ. Cal. Publ. Bot. **10**:
  414. 1924.
  Vincetoxicum Lundellii Standl. Field Mus. Publ. Bot. **8**:
  148. 1930.

Gonolobus **dasystephanus** (Blake) Woodson, comb. nov.
  Vincetoxicum dasystephanum Blake, Contr. Gray Herb.
  52: 84. 1917.

Gonolobus **Lasiostemma** (Hemsl.) Woodson, comb. nov.
  Lachnostoma Lasiostemma Hemsl. Biol. Centr.-Am. Bot.
  2: 335. 1882.

Gonolobus **oblongifolius** (Donn.Sm.) Woodson, comb. nov.
  Trichostelma oblongifolium Donn.Sm. Bot. Gaz. **48**: 296.
  1909.

Gonolobus **stenanthus** (Standl.) Woodson, comb. nov.
  Vincetoxicum stenanthum Standl. Field Mus. Publ. Bot.
  4: 255. 1929.

Gonolobus **stenosepalus** (Donn.Sm.) Woodson, comb. nov.
  Fimbristemma stenosepala Donn.Sm. Bot. Gaz. **18**: 208.
  1893.

SUBGENUS 3. PSEUDOLACHNOSTOMA

Gonolobus **arizonicus** (A.Gray) Woodson, comb. nov.
  Lachnostoma arizonicum A.Gray, Proc. Amer. Acad. **20**:
  296. 1885.

Gonolobus **gonoloboides** (Greenm.) Woodson, comb. nov.
  Lachnostoma gonoloboides Greenm. Proc. Amer. Acad.
  39: 84. 1903.

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IX. Marsdenia R.Br. Mem. Wern. Soc. **1**: 28. 1809.

Nephradenia Dcne. in DC. Prodr. **8**: 604. 1844.
Ecliptostelma Brandg. Univ. Cal. Publ. Bot. **6**: 371. 1917.

I have been unable to find characters to distinguish *Neph-
radenia* except the erect, fruticose habit. *Ecliptostelma molle*

Brandg. (loc. cit. 1917) is identical with *Marsdenia Gilgiana* Rothe, which seems to be an extraordinarily variable species, even from the present meager representation, and which possibly should be merged with the very closely neighboring *M. mexicana* Dcne. For further generic synonyms, reference should be made to the monograph by Rothe (in Engl. Bot. Jahrb. **52**: 354–434. 1915). Following that standard work, new sections or subgenera probably will have to be erected to include both the following species, although I am deferring that action for the present.

MARSDENIA **astephanoides** (A.Gray) Woodson, comb. nov.
   Vincetoxicum astephanoides A.Gray, Proc. Amer. Acad. **22**: 435. 1887.
   Cynanchum astephanoides (A.Gray) Standl. Contr. U.S. Nat. Herb. **23**: 1177. 1924.
MARSDENIA **neriifolia** (Dcne.) Woodson, comb. nov.
   Blepharodon neriifolium Dcne. in DC. Prodr. **8**: 604. 1844.
   Nephradenia neriifolia (Dcne.) Benth. & Hook.; Hemsl. Biol. Centr. Amer. Bot. **2**: 336. 1882.
   Nephradenia fruticosa Donn. Sm. Bot. Gaz. **16**: 196. 1891.

TWO NEW ASCLEPIADS FROM THE
SOUTHWESTERN UNITED STATES

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ASCLEPIAS **Ruthiae** Maguire, spec. nov. Herbae perennes; caudices multicipitales, caulibus nonnullis simplicibus suberectis 1.0–1.5 dm. altis crispo-pilosulis; folia opposita vel approximata late ovata apice aut acuminata aut abrupte mucronulata basi obtusa 2.2–4.5 cm. longa 1.5(1.0)–2.3 cm. lata, lamina sparse margine densius pilosula, petiolis 0.2–0.5 cm. longis minute pilosulis; inflorescentia aut terminalis aut lateralis umbelliformis pauciflora (2–7) sessilis, pedicellis filiformibus 1.5–2.5 cm. longis pilosulis; calycis lobi lanceolati acuti 0.2–0.3 cm. longi pilosuli violacei; corolla rotata pallide cano-violacea extus minute puberulo-papillata, lobis ovatis obtusis ca. 0.4 cm. longis patulis; staminum columna ca. 0.1 cm. alta viridula inter foliolas coronae saccata, antherae purpureae 0.15–0.23 cm. longae apicibus scariaceis obtusis integris; pollinia compresse elongato-pyriformia ca. 0.05 cm. longa; coronae foliolae saccatae ca. 0.2 cm. longae lobo dorso obtuso lobulis lateralibus obtusis longiore corniculo incluso roseo-purpureae; folliculi erecti falcate ovato-fusiformes 3–4(5) cm. longi dense pilosuli vel subglabrati.

UTAH: frequent, sandy soil, vic. water tank, Calf Springs Canyon, alt. 5000 ft., San Rafael Swell, 18 mi. southeast of Castle Dale, Emery Co., May 10, 1940, *Ruth & Bassett Maguire 18310* (Herb. Utah State Agricultural College, TYPE; Herb. Missouri Bot. Garden, ISOTYPE); Calf Spring Canyon, San Rafael Swell, June 5, 1940, *B. Maguire 18423* (Herb. Utah State Agr. Coll.; Herb. Missouri Bot. Gard.); same locality, June 7, 1940, *B. Maguire 18477* (Herb. Utah State Agr. Coll.;

(245)

Herb. Missouri Bot. Gard.); in the desert, 20 mi. south of Green River, June 8, 1939, *C. L. Porter 1799* (Rocky Mtn. Herb., Univ. Wyoming).

This is another member of the complex represented by *A. brachystephana, A. uncialis,* and *A. Cutleri* (cf. Woodson, Ann. Missouri Bot. Gard. **26**: 262. 1939), but is distinguished by its broadly ovate leaves and short lateral hood lobules. It

Fig. 1. *Asclepias Ruthiae* Maguire. Flower, pollinia, and hood in longitudinal section.

gives me much pleasure to dedicate it to my wife, Ruth R. Maguire, who was its discoverer and who so frequently is my helpful companion in the field.

ASCLEPIAS **Sperryi** Woodson, spec. nov. Herba suffrutescens ramosissima ca. 1.5 dm. alta habitu *A. macrotem* simulans; caules gracillimi suberecti compositi minutissime pilosuli vel glabrati, internodiis ca. 1.5–2.0 cm. longis; folia linearia 1–5 cm. longa ca. 0.05 cm. lata sessilia glabra; flores solitarii laterales, pedicellis ca. 1 cm. longis glabris; calycis lobi ovato-

lanceolati acuti 0.2–0.25 cm. longi papillati; corolla dilute
viridula plus minusve purpureo-tincta, lobi ovato-elliptici acuti
0.5–0.6 cm. longi patuli; staminum columna vix manifesta, co-
rona sessili; gynostegium ca. 0.3 cm. altum, antheris 0.1 cm.
longis apicibus scariaceis inflexis, stigmate depresso ca. 0.25
cm. diam.; coronae foliolae habitu flosculo *Aristolochiae*
similes gilvae vel dilute roseae dense papillatae parte basali
patula ca. 0.2–0.3 cm. longa involuta margine alata corniculo
umbonato incluso, parte superiori erecta laminata apice 3-
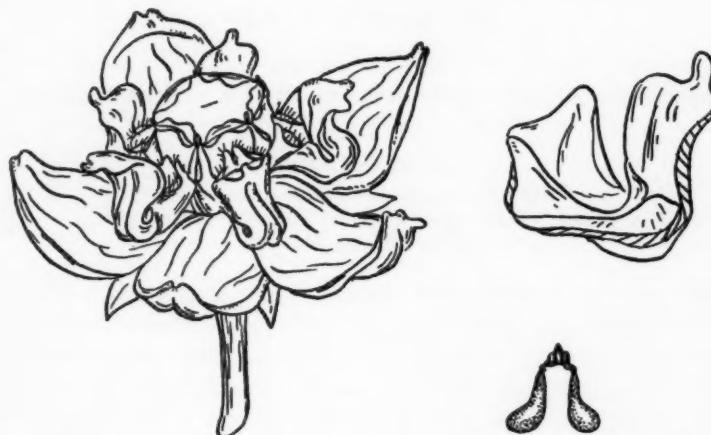

Fig. 2. *Asclepias Sperryi* Woodson. Flower, pollinia, and hood in longitudinal
section.

lobulata; folliculi deflexi anguste fusiformes ca. 6 cm. longi
0.5 cm. crassi laeves glabri.

TEXAS: east of Nichols Ranch House, Glass Mountains,
Brewster County, Aug. 1, 1938, *C. La Motte, O. E. Sperry, &
B. H. Warnock T553* (Herb. Missouri Bot. Garden, TYPE;
Herb. Sperry, ISOTYPE); about 10 miles east of Alpine, Brew-
ster County, May 21, 1936, *Sperry T301* (Herb. Missouri Bot.
Garden; Herb. Sperry).

The superficial habit of this species is almost identical to
that of *A. macrotis,* but the 1-flowered cymes and peculiar form

of the corona hoods are quite exceptional in the genus as represented in North America. It has been named for Professor Omer E. Sperry because of his activity in the botany of western Texas and in appreciation for his aid to my study of *Asclepias*.